

Deleterious behaviorally transmitted traits in equilibrium

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Abstract. Background: This paper investigates the propagation of behaviorally transmitted traits with negative effect on host fitness. **Methods:** We analyze equilibrium between genetically transmitted and behaviorally transmitted competing propagators and consider whether a behavioral propagator is linked to reproduction (e.g. vertical culture transmission), or not. We employ combined genetic and behavior-induced fitness components for hosts, while behavioral propagators have replication factors to distinguish from what's good for the host (fitness). **Results:** A trait which spreads faster than its marginal host fitness contribution reduces population will establish itself. The often transient nature of laterally transmitted traits may be a defense against accumulation of deleterious traits. Laterally transmitted traits with high spreading rate often do not equalize with genetic traits, spreading outside natural selection of the hosts. Vertical transmission reduces replication rate and allows group selection against deleterious behaviorally transmitted traits. Competing mutually exclusive propagators contribute to inequality and altruism, but compete through adverse fitness since exclusivity assumes low conversion. **Conclusion:** Behaviorally transmitted traits, in some cases a tremendous advantage, may also be a significant problem in the development of societies.

Keywords: culture, co-evolution, meme, altruism, natural selection, competitive equilibrium

1. Introduction

The goal of this paper is to demonstrate the theoretical ability of deleterious lateral behaviorally transmitted traits to establish themselves in a population, and to characterize various cases, dilemmas and defenses arising. Examples include pseudoscience (e.g. Lowell's canal sketches of Mars and Venus), political and economic ideologies which produce less than promised, lifestyles that don't include childbearing, technologies with unintended effects, and destructive addictions that spread from person to person exploiting the platform of their hosts like a virus. Will they be deselected by natural evolution in the way insects build resistance to pesticide? Do they follow the rules for genetic deleterious (altruistic) behavior? Or is there new mathematics for a 2nd replicator not tightly linked to host fitness?

Behavioral transmission has been addressed in the context of gene-culture co-evolution, [1-3] also known as dual inheritance, [4] and closely related to niche construction. [5] The term "meme," coined by Dawkins in 1976 as a unit of cultural transmission [6] at first attracted some of the same investigators who proposed a population-genetics like calculus. [7] Since 2005 co-evolution is largely the paradigm for evolution, and memetics is an information science. [8] Blackmore suggests selection pressure favored those that made good choices regarding who or what to imitate, and imitated intelligently. [9] This positive bias is a claim we investigate. Using a dual replicator model with host (carrier) induced fitness as a separate factor from self-replication efficiency, the possibility of evolving deleterious (maladaptive) traits was noted by Aguilar and Akçay. [10] Our analysis

extends this result and examines the evolution of defenses against deleterious behavioral trait transmission

We define the point of view of this paper and historical context as follows. Though having existed earlier, evolution of cultural factors was re-popularized in the mid-1970s under the headings of sociobiology and memetics. Philosophical and technical objections led to the specialization of memetics as the study of propagating information without a necessary cultural effect, though it is often intended to influence behavior (e.g. commercial and political memes). [8] Co-evolution and niche construction brought culture and genetics so close together it is nearly as difficult to imagine deleterious traits evolving as with genetics alone. However, as noted Aguilar and Akçay showed how this can happen. [10] We take the point of view there is a second nearly-independent extragenetic replicator, and reproduce not only Aguilar and Akçay's result with a simpler development, but other quantitative results on group formation and the evolution of exclusivity, etc. We do not ask readers to change their points of view; only to consider this point of view's explanatory power for the duration of this paper.

We could use another term such as "extragenetic" (already in use, very generally) or invent something new. But for convenience and consistency we instead use the term "meme" as Dawkins originally conceived it (not in the pure information sense) for the longer "behaviorally transmitted trait" though our methods are more akin to co-evolution (see 3.1 for differences in emphasis). While the difficulty of defining a physical embodiment of the replicator remains, it is no more an obstacle to analysis than lack of understanding of DNA was to Mendel.

This paper studies deleterious traits. In practical cases it may take years, centuries or longer to determine whether traits are deleterious, but we only consider long term equilibrium. For instance, are the internal combustion engine and its uses (a rather large complex of traits) advantageous or deleterious? It seemed wonderful and now there is an effort to abandon it. Fast food saves time but is thought by some to have health effects. Regions where kosher and halal traditions dominate resist the introduction of fast food, while other regions do not. Cell phone use permeates virtually all areas of the planet, while economic and political behavior complexes are often mutually exclusive of one another. This exclusivity feature is something we will study.

Using meme-gene and meme-meme equilibrium we derive conditions for evolutionary modes of interest. We will show a behavioral trait as its own replicator is rather weakly linked to the fitness of the host as regards host replication, *unless* groups remain small and transmission is largely vertical (cultural), to offspring in the group. The occasional advantage of a laterally transmitted trait already vetted by group selection establishes positive selection for behavioral transmission despite its risks to individual groups. The following literature discussion will be taken as empirical findings with which we should be consistent, and includes material from both co-evolution and memetics.

Behaviorally transmitted traits are not the first evolutionary instance of lateral trait transmission. Bacteria are able to hand off genetic material independent of the reproductive process. Evolution largely suppressed this kind of lateral transmission between co-equal complex beings. It remains as viral pathogens and in rare cases an evolutionary step, such as the inclusion of mitochondria into eukaryotic cells, or the use of the Arc protein in mammalian memory which may be a repurposed retrovirus. [11]

Log normal distribution has been found for fast-spreading memes, [12] implying likelihood they spread by a stochastic growth process. Models of fast-spreading/dying memes often need to be complex and typically there is an explosive rise to some limit of popularity and then a slower but still rapid decay. [13] The characteristics of spread and decay, occasional repetition of prior memes,

perception of harm from many memes, and instinctive use of words like viral and contagion by the public have led to serious use of epidemiological models to describe meme propagation. [14]

Sterelny emphasizes lasting cultural aspects and distinguishes three mechanisms: (a) niche construction leading to group selection, (b) vertical flow of information from parents to children, (c) replication and spread of memes. [15] He argues the first two are definitely important in establishing lasting change, but spread of memes only *might become* important. The essential difference between (b) and (c) is vertical vs. lateral spreading, and that is where we find deleterious effects.

Lateral transmission is similar to the spread of a pathogen, which implies some kind of harm that is expunged by an immune-like reaction. It can be considered against studies that find social media and attendant meme propagation to increase sub-group formation, isolation and polarization, such as their use in the delegitimization of 2016 US presidential candidates. [16] Fast-spreading ideas if given weight can cause revolutions and formerly were associated with words such as propaganda and ideology. The BBC reports 20% of “viral misinformation” comes from celebrities but accounts for 69% of engagement. [17]

Studying memes in connection with culture creation, Atran concludes that “unlike in genetic replication, high-fidelity transmission of cultural information is the exception, not the rule.” [18] A study comparing informational (truth, moral lesson) vs. emotional (disgust) factors in meme propagation found that greater disgust (ingestion of a contaminated substance) resulted in greater propagation. [19] Non-local media generally and Internet memes particularly may be thought of as lateral (or horizontal) as opposed to vertical cultural transmission, exposing people to ideas outside their local society that they would have rarely encountered centuries or millennia ago. But, as recently as 2019 it was found that geography is still important in transmission of Internet memes. [20]

Lynch and Baker concluded from an analysis of birdsong memes that increased variability in memetic transmission support “high levels of among-population differentiation . . . in spite of high levels of migration . . . [allowing] accumulation of new mutants in different populations before migration can disperse them.” [21] One supposes increased migration along with faster meme-driven group formation will affect human populations, part of which Ross and Rivers already found. [16]

Meme competition has been studied empirically and through simulation. Nogueras and Cotta compared good and bad memes in networks and in panmictic spreading and concluded the “increased takeover time” associated with the non-panmictic topologies is “essential for improving the chances for good memes to express themselves in the population by improving their hosts,” and that performance enhancing memes are more successful in spatially structured spreading (c.f. geography finding above) than in the panmictic case. [22]

Weng et. al. used competition for limited individual and collective attention to find support for “heterogeneity in the popularity and persistence of memes . . . without the need to assume different intrinsic values among ideas.” [23] From limited user attention Gleeson et. al. derived heavy-tailed distributions of meme popularity. [24] More recently Spitzberg attempted a comprehensive model able to forecast numerous meme features based on competition “at multiple levels to occupy information niches.” [25]

The agency aspect of social learning agrees with Atran’s thesis that processing by a multimodular mind (one created by evolution) reduces the fidelity of transmission and creates constant, rapid mutation, especially when processed by children. [18] However, systematic study does support the idea that children irrationally mimic their parents’ choices (for example in food).

[26] In a social learning study, Wisdom, et. al. show that “participants combined multiple sources of information to guide learning, including payoffs of peers’ solutions, popularity of solution elements among peers, similarity of peers’ solutions to their own, and relative payoffs from individual exploration.” [27] The study further finds that “when peers’ solutions can be effectively compared, imitation . . . can also facilitate propagation of good solutions . . .”

Social learning can also be non-rational in a strict sense. A long standing puzzle is human behavior in an ultimatum game in which one person proposes how to divide a pool of money, and the other decides to accept, or reject in which case no one gets anything. Game theorists claim it is rational to accept very small portions, but actual human participants rarely settle for less than 40%, perceiving less is unfair. Zhang shows how social learning in an environment in which there are strategies and mutations contributes to this real world outcome. [28]

Social learning is often associated with the evolution of cooperation in games such as Prisoner’s Dilemma and public goods. While it was initially assumed to be a primary enabler of the evolution of cooperation, Burton-Chellew and associates have been showing that as people learn about game theory they decrease their cooperation, and social learning has a specific role in this. [29-30] Support for this comes from a demonstration that cooperation by the poor with the wealthy can lead to an increase in wealth inequality. [31]

2. Approach

We reserve the word “fitness” to describe the ordinary reproductive success potential of a meme host. The spreading rate of the meme is called replication factor, and includes a statistical average of the sort of individual preferences social learners might express in their choices. A fast-spreading meme may reduce the fitness of its hosts, and this we explicitly model. Exactly how the meme is connected to ordinary reproductive fitness will determine the course of natural selection, not the replication ability of the meme alone.

There is not necessarily a concept of “generation” with behaviorally transmitted traits. While vertical culture transmission may align with generations, lateral transfer may not.

We define a behavioral trait **replication factor** R_M which is based on a **time period** T . Depending on the speed of a trait’s propagation, the time period could be a month, a year, whatever is convenient. The replication factor is the number of new instantiations of the meme in a host created from each existing instantiation in a single period T . If propagation is allowed to run its full course, the period T can be variable, such as time until the next mutation. Usually in our case the host is a human, but it could be a computer, bird, anything over which a behavioral trait has influence. We assume there is some intrinsic replication rate based on the social learning appeal and difficulty of transmission, which is represented via the replication factor.

The **population of hosts is** P , and the **instantiations of the behaviorally transmitted trait in** P is P_M . Denoting the number of instantiations at the end of the period as P_M' and neglecting for the moment population change over the period we can write:

$$(1) \quad P_M \leq P$$

$$(2) \quad P_M' = \text{Min}\{P_M(1 + R_M), P\}$$

We will cease writing the “Minimum” constraint for brevity, though it is implicit. It is evident that the meme does not *directly* have the power to increase or decrease population P . It must act through genetic traits to accomplish that.

Our first step will be to explore the relation between genes and memes. Behaviorally transmitted traits are phenotypic traits without an analytic molecular basis. For comparison to genetic traits it should be sufficient to use a phenotypic approximation to population genetics. Initially we consider a dominant and heritable trait or trait complex. Later we will discuss recessive traits of either type. Dominant traits are always visible. We count **trait instantiations** P_G within hosts as the relevant factor of interest. Thus we have a constraint similar to (1) on P_G :

$$(3) \quad P_G \leq P$$

We assume an **average population growth rate of** R_p , prior to meme introduction and including mortality if needed, and to be defined over time interval T rather than generationally, thus:

$$(4) \quad P' = P(1 + R_p)$$

This brings us to the question of fitness. For our gene-meme comparison, we need to set up a competition. We thus assume the genetic trait of interest has a positive beneficial fitness. Here again we must adjust from a general time base, in which fitness is usually defined, to the period time base. Let **F_G be the excess instantiations of the genetic trait of interest**, over and above R_p , in one period. This includes not only the usual idea of fitness conferred to an individual by the trait, but the statistics of its heritability since it is trait instantiations not individuals being computed.

For convenience we let average population growth be zero: $R_p=0$ so that **$1+F_G$ is the relative per period increase in the genetic trait**. What's important is not that the population is in equilibrium with its environment, but that we are only interested in the relative changes caused by the gene complex of interest, and the invading meme. The spread of the genetic trait per period is given by:

$$(5) \quad \begin{aligned} P_G' &= P_G(1 + F_G) \\ \Delta P_G &= P_G' - P_G = F_G P_G \end{aligned}$$

The **meme induced (or conferred) fitness (of the host, not of the meme) is assumed to be $-F_M$** , with the minus sign explicit to remind us of its deleterious nature. This sets up a competition. Otherwise it would be beneficial for both the genetic trait of interest and the meme to spread among the whole population. We can now write:

$$(6) \quad P_M' = P_M(1 - F_M)(1 + R_M) = P_M(1 - F_M + R_M - F_M R_M)$$

Removing the second order term $F_M R_M$ and writing for the change in meme instances:

$$(7) \quad \Delta P_M \approx P_M(1 - F_M + R_M) - P_M = (-F_M + R_M)P_M$$

The $R_M P_M$ components are conversions. The $-F_M P_M$ term is a presumed loss of individuals if the induced fitness from the behaviorally transmitted trait is deleterious.

3. Development

3.1 Panmictic Meme-Genes Equilibrium

We proceed by assuming the population frequencies for two competing traits are changing from selection pressures, one genetic and one behaviorally transmitted, and derive equilibrium conditions between the two traits. There are two conditions for full equilibrium. First is population equilibrium, in which the number of individuals does not change. Physical ΔP is set to zero and conversions ignored. Combining (6) and the physical part of (7) we have:

$$(8) \quad \Delta P_G - F_M P_M = 0 \rightarrow F_G P_G = F_M P_M$$

The second equilibrium condition is cessation of spread of the meme, which is realized when the meme hosts die as fast as the meme infects (converts) new ones:

$$(9) \quad R_M P_M - F_M P_M = 0 \rightarrow R_M P_M = F_M P_M$$

Population equilibrium (8) is achieved when the population growth from the new gene is offset by the population loss from the deleterious meme. If no new factors oppose the meme, its condition for spreading from (9) is $R_M > F_M$. If it spreads faster than it kills, it will reach 100% penetration irrespective of F_G .

The effect of the behavioral trait upon genetics would be of primary importance in co-evolution. Here we assumed the same fitness impact with or without the new genetic trait G , which focuses on the solitary effects of the behavioral trait and minimizes co-evolution. Comparing the new genetic trait to the old baseline we have by definition a fitness ratio of $1 + F_G$, and the behavioral trait affects both equally at $1 - F_M$. If we suppose the genetic trait G is better adapted to the behavioral trait M , setting up for co-evolution with combined fitness F_{GM} and a fitness ratio $1 + F_{GM} > 1 + F_G$, then selection pressure between the new genetic trait and the baseline is increased by the behavioral trait. Such an increase in selection pressure between neighboring hominid species due to a cultural facility factor has been proposed. [32]

If population equilibrium is obtained *before* the meme achieves 100% penetration, *and* panmictic meme transmission allows it to reach the entire host population, *and* the meme induced fitness for the host is deleterious in a population fitness sense, *and* if no other factors change the intrinsic population growth factors (recall we assumed it was initially in equilibrium), *then* the population theoretically declines until it is extinct. There is nothing selection alone can do to stop it. Evolution can stop it by introducing a new gene or meme with sufficiently positive fitness boost, but this does not eradicate the meme. It becomes memetic load, like genetic load.

We call this **meme extinction risk**, the risk of extinction from deleterious memes whose propagation is not checked by natural selection, because they spread faster than their hosts die. Further it is cumulative. A negative balance in incoming meme induced fitness and average $R_M > F_M$ will eventually cause extinction. We will discuss counter strategies below.

Notice the presence of conditions which make problems hard to detect. It's hard to identify the source because correlations are displaced in time. Symptoms are relieved when the population is in equilibrium. But as the meme spreads equilibrium is again lost. There is a delay built into the system which confounds most kinds of control loops, natural or created by the species.

3.2 Vertical Transmission of Memes

Instead of panmictic transmission of the meme, we now assume vertical transmission along with reproduction, confined to a small cultural group. After N periods children mature and some number mate into out groups. They can carry the meme with them and infect new groups. Otherwise there is little contact between groups and no meme transmission.

This condition reduces meme transmission approximately by some parameter of the order of N . We assume the meme replication rate is applicable only during one of N periods. Then we have new equilibrium conditions:

$$(10) \quad P_M R_M / N = F_M P_M$$

Aside from the immediate benefit of reducing the meme replication rate by an order of magnitude, group selection comes into play. A fast-spreading meme will easily establish itself in a small group, and if deleterious, the performance of that group will suffer. They may lose a battle, or be ostracized from mating, and the meme may not spread at all outside the group. These chance events are difficult to quantify and model, so we leave it at equation (10).

By allowing group selection to filter memes, this delay in transmission produces the effect observed by Noguera and Cotta that non-panmictic meme propagation allows time for “good memes” to distinguish themselves by improving their hosts, [22] or for the quality of peers’ solutions to become evident. [27]

3.3 Passive Defensive Conditions

The use of vertical culture transmission may be a meme itself. Modifications to it may well be deleterious. This approach also inhibits the spread of useful ideas, and is discriminatory. Many people currently advocate abandoning suspicion of vertical culture.

There is selective pressure in the vertical culture system to increase generation time, at least with respect to modulating meme transmission. In the U.S. average age of marriage has increased from 20 to 27 years since 1950. [33] Marriage age has other constraining factors. In 1985 marriages beyond the late 20s were less stable due to inadequate role performance. [34] The Institute for Family Studies reports stability now increases into the 30s. [35] Increased generation time can be used to impart more complex culture which might have less deleterious or even positive fitness.

A more targeted criterion might be to limit the lifetime of laterally spread memes. This amounts to positing directly the transient behavior of Internet memes. Limited lifetime memes will overlap less and have lower cumulative effect. Perhaps faster spreading memes would have the shortest lives. Perhaps boredom is an instinct developed in part as meme defense.

These are passive defenses. Evolution of active meme exclusivity will be addressed below.

3.4 Special Cases of Non-Linear Meme Interaction Can Emulate Genetics

A simple case of meme-meme interaction is suppression of one of the memes. Morality and compassion memes demand suppression of selfish impulses. Fairness memes demand we treat others as we would like to be treated, and we have seen that such a fairness meme apparently overrides rational application of game theory in the ultimatum game.

Another reason for suppression may be the source of a meme, e.g. from a culture that is under suspicion, or a parent or other caregiver not the favorite of the child.

Still another reason is the duality of vertical inheritance. A child receives cultural (vertical) memes primarily from two parents, and secondarily from other members of the culture group. Much of the time those other members will be associated with one parent or the other, for example family members or business and trade associates. So if memes are not expressed evenly in the society then the child gets two sets of memes, a mother set and father set. Many memes are mutually exclusive to some degree just because of time and energy costs.

It is possible then to have a situation of dominant and recessive memes. Observable traits can also be influenced by many memes. For example honesty may be influenced by ethical, religious, rational and cooperation memes. This sounds like a continuous trait. So it may be appropriate to use some of the techniques of conventional population genetics.

3.5 Behaviorally Transmitted Trait Competition Analyses

We now consider behaviorally transmitted traits that are hostile to each other. For the moment we *assume* these memes are exclusive, that each will not spread among a population that adheres to the other. Later we derive the *evolution* of exclusivity. In this section we first analyze it. This leaves the method of competition to consist of affecting the relative fitness of hosts.

Each meme already has an induced fitness factor relative to its own hosts. In addition each may induce its hosts to work to actively reduce the fitness of the hosts of enemy memes and/or the enemy meme's replication factor, by physical means. The means could range from giving them a bad reputation, ostracizing them (c.f. cancel culture), removing their employment, putting them in concentration camps, terrorizing them, to conducting military campaigns.

This reduction comes at a cost to the meme hosts enforcing it. Invading memes are sometimes an existential threat, but do they provide a reservoir of increased payoff with which to fund enforcement action? In games such as Prisoner's Dilemma and public goods the punishment cost is offset by greater game rewards due to cooperation. In a meme conflict the burden of multiple deleterious memes is reduced by eliminating some of them. If common behavioral traits allow interaction of larger groups, then the opportunity to achieve some cooperation payoff may exist. But the cost of meme conflict may also be supported by simple extortion and exploitation of the losers. We do not suppose that such justification always exists. If it did, we might suppose the behavior spread was rational and not deleterious, at least to its spreaders. Rationality is a more elusive concept in the context of reproductive fitness than in the context of economics.

We assume the competing memes, $M1$ and $M2$, will not be expressed in the same host. The hosts will choose sides.

Let K_1 be a reduction in fitness imposed on $M1$ by $M2$, C_2 be the fitness costs incurred by $M2$ in doing so, and vice versa for K_2 and C_1 . Further, let the actual fitness reduction/cost be proportional to the ratio of host populations, and let the reductions apply equally to replication factors and induced fitness. The modification factors are then $K_1 C_1 P_{M1} / P$ and $K_2 C_2 P_{M2} / P$. Note that the total population is the *relevant* population. Perhaps it is only local population for a tribal dispute. Only in world campaigns is it the world population.

An advantage of our symmetric phenotypic treatment of genetic and behaviorally transmitted traits is we can rewrite the gene-meme equilibrium condition (8) for **two memes** by substituting $F_{M1} P_{M1}$ for the genetic term $F_G P_G$:

$$(11) \quad F_{M1} P_{M1} = F_{M2} P_{M2}$$

And add the fitness reductions/costs:

$$(12) \quad F_{M1} P_{M1}^2 K_1 C_1 / P = F_{M2} P_{M2}^2 K_2 C_2 / P \\ \Rightarrow F_{M1} P_{M1} = F_{M2} P_{M2} (P_{M2} / P_{M1}) (K_2 C_2 / K_1 C_1)$$

Spreading equilibrium is not meaningful if exclusive memes have already saturated the population so we do not show a spreading equilibrium. Equation (12) has been rearranged to look like (11) with all the modifications on one side. Total population P divides out entirely (though not necessarily if the parties face asymmetric external relevant populations). The meme host population ratio reflects an advantage to the larger meme host population. The ratio of fitness reductions to costs reflects tactical, strategic and raw physical or technical ability advantages.

If the sides are nearly balanced, the war is a dead cost with no benefit.

If significantly unbalanced and large fitness reductions can be inflicted to make a short war, then game theory logic dictates the side with advantage compares the induced fitness reduction from allowing invasion of the other meme, to its costs in conducting the war. For example, P_{M2} would incur fitness reduction F_{M1} if they allow $M1$ to invade. They would incur this indefinitely. If they wage war they incur $(P_{M2}/P_{M1})(K_2C_2/K_1C_1)$ for a limited time. Let's consider two cases:

- a) If $M2$'s advantage is primarily population, they are already ahead and it may not take long to reduce the remaining P_{M1} to surrender (perhaps they will give up their meme or at least agree not to evangelize it). This is the case of conventional war by a major power.
- b) If $M2$'s advantage is primarily ability to impose greater costs than they receive, the war will take a long time and they will not be able to control its termination date. This is a situation of asymmetric war against a more numerous power. The objective is to be so annoying the more numerous power agrees to back off and not export its meme.

In both cases we consider that the result may stop short of extinction if agreements about meme spreading can be reached. This is theoretical. The author makes no claim that such agreements are achievable or enforceable. In the Cold War both sides aggressively exported their memes. When it ended, Russia did not cease as a major power, give up state control of major corporations, and in the long run did not cease expanding its hegemony. It quit selling communism.

Returning to the balanced situation, note that one can hide behind iron or bamboo or capitalist tariff/security curtains, but memes will eventually propagate anyway. If one side obtains a slight advantage, a credible threat of some version of war may persuade the other either to adopt the competing meme, if they can be persuaded it is not so deleterious, or mutual agreement may be reached for neither side to export their memes to the other side, along with agreements to manage population growth and resource consumption to avoid future conflict. This becomes a cooperation game, and there will be many "rounds" with cheating, punishment, and so forth. It is difficult to enforce such an idea in a free society where individuals and corporations may persist in exporting their memes.

While much of this may strike the reader as not new, it maps what is already well known into our model of behaviorally transmitted traits and their spread and interaction with population genetics. We have claimed almost every non-genetic aspect of society other than resource holdings is some kind of meme. If our theory had not been able to reproduce these commonly understood generalities, it would be in trouble.

3.6 Special Cases – Inequality, Power, Truth, Acceleration and Altruism

In competing exclusive meme equilibrium, if we assume that most new converts will occur vertically among the newborn (not always true) then we can examine several interesting cases by looking at the population fitness factors. Rewriting (13) for their ratio:

$$(13) \quad F_{M1} / F_{M2} = (P_{M2}^2 / P_{M1}^2)(K_2C_2 / K_1C_1)$$

If equation (13) is nearly balanced then changes in imposed and incurred costs will govern. Non-exclusive memes are easily invaded by exclusive memes because they offer no resistance. Eventually random mutations will produce a competing exclusive meme. Losing memes would either vanish before effective memes that exclude them, or the stimulus to exclusion might "kick in" when some threshold of threat was met, either a sign of extreme exclusivity in the lesser populated meme, or a threatening spreading rate. We might expect to find one of the following cases for a pair of competing memes if at least one of them is exclusive of the other:

- a) One meme dominates and the other either vanishes or exists below the threat threshold.
- b) The memes exist in a near balance so that (13) is approximately satisfied.

The following discussion is limited to case (b), near balance, and observes the condition for changing the balance. The result of the change in fitness factors will be a change in meme host population, tipping the balance one way or the other.

WEALTH INEQUALITY: Consider a mutation $M1'$ of $M1$ which changes either incurred or imposed costs. We assume the variant initially is accepted as non-exclusive within $M1$. It will freely propagate in the $M1$ host population but not in $M2$. We might create a wealth accumulation meme within the general capitalism meme by using the idea of reducing the number of children in order to make each more wealthy. Then the wealthy version $M1'$ incurs a higher fitness cost C_1' . If $M1'$ spreads widely in the population of $M1$ -type hosts then $M1$ population declines relative to $M2$ by the factor C_1'/C_1 from direct cause, and then declines further as described below. We wouldn't expect this population fitness effect to completely explain inequality. It is just one contributor.

POWER: In the above case as P_{M1} decreases, the ratio P_{M2}^2/P_{M1}^2 rises while F_{M1}/F_{M2} has fallen. With this positive feedback P_{M2} will continue to rise and P_{M1} will decline to a very small fraction of the population. This may halt when P_{M1} realizes the existential threat and/or sufficient wealth allows P_{M1} to again increase its reproduction rate. If P_{M1} becomes extremely small then it continues to exist only at the pleasure of P_{M2} unless it also accumulates power of some kind. Thus wealth accumulation memes are likely to include beliefs or techniques about power.

TRUTH: Wealth up to now is an extraneous factor in our model, acting only through costs of acquiring it. The same is true of "truth." Suppose consuming a certain substance (e.g. alcohol) increases reproduction rate, but causes wealth to decline (accidents, poor health or judgment). A meme which exposed this relationship (a truth meme) would remove the reproductive advantage if adopted. So the truth meme would incur a cost and decline just as did our wealth meme.

ACCELERATION: A meme might encourage accumulating resources which can be used to accelerate the natural replication rate. For example the wealthy who become celebrities attract a disproportionate share of social media engagement with their ideas [17]; wealth can be used to buy space in media channels which enhances transmissibility [23-25]; fame (e.g. from acting or sports) can translate into the ability to get votes; wealth can allow time to devote to politics. There likely are thresholds of effectiveness involved, but taking a simple linear approach we define an acceleration factor $A1$ associated with $M1$ which accumulates separately over time at rate R_{A1} . Let $A1=1$ at period zero. When $M1$ initially appears its propagation is given by (7) but after N periods becomes

$$(14) \quad \Delta P_M(N) \approx (-F_M + R_M(1 + R_{A1})^N) P_M$$

Conversely a meme which promotes loss of a useful resource incurs a decrease in spreading effectiveness. This is the supposed dilemma of socialism in competition with capitalist societies, and a possible driver of long alternating cycles in society.

COMPETITIVE ALTRUISM: Now we introduce a variant of $M1$ called $M1'$ which has an incurred cost increase in $C_1' > C_1$ as did the wealth meme, but also increases the imposed costs $K_2' > K_2$ on the $M2$ population. If the following condition is met, other things unchanged, this variant increases P_{M1}/P_{M2} :

$$(15) \quad K_2' / C_1' > K_2 / C_1$$

Notice that the incurred fitness costs may mean that certain members of the $M1$ population will die before reaching their reproductive potential. The $M1'$ variant can spread laterally within $M1$ and does not require any children to do so. We've already established that a non-exclusive meme

can spread and become permanently lodged in a population even if it is deleterious.

However, if (15) is met the population of $M1$ hosts increases. This may even aid lateral spread of $M1'$. Altruism can exist for this case without kin or group selection, though there must be a competing meme for it to have a material advantage. This is subject to the mutual exclusivity assumption, which confines memes to mostly vertical propagation. Thus, it is not useful as a conversion defense, only in exclusive meme defense. Other altruistic cases will emerge below.

3.7 Evolution of Exclusivity

We can use the technique of the previous section to analyze the evolution of memes with exclusivity. We assume there are discrete mini-meme variants of a general meme idea, representing *either* actual variation in the memes *or* variation in host implementations of them. They are non-exclusive of other meme variants within the same general meme idea until some threshold of distinction is reached, which does not concern us at the moment.

These will spread within the host population which doesn't exclude them, but since they express degrees of action they cannot all be dominant primary memes. We make a significant assumption in the interest of analysis, that *the most evolutionary advantageous meme (conferring the greatest host fitness) is the most frequently expressed form*. This can be argued from a social learning point of view, that people will likely copy the most successful memes. And it can be argued from a strict evolutionary point of view, that if holders of a certain meme have more children over generations they will come to dominate.

Neither is entirely true. If large families in financial hardship are the most reproductively fit, still not everyone may copy that meme. Since within a non-exclusive group of mini-memes we cannot guarantee vertical transmission, children may not express the same meme variant as parents. So this second assumption may produce results which are somewhat but not entirely true when compared with empirical data. Its use does not affect whether larger meme increments are supportable once established, only the analysis of their evolution in small increments.

Consider a meme $M1$ established in a population of hosts and an invading meme $M2$, bringing with it a fitness burden F_{M2} . By chance or other means there appears a variant $M1'$ opposed (or more opposed) to $M2$ so that $K_2' > K_2$. It brings to bear imposed fitness K_2' against $M2$, and incurs cost C_1' from doing so. The already established $M1$ primary variant already imposes and incurs costs K_2 and C_1 .

The fitness difference between $M1$ and $M1'$ is given by the difference between K_1C_1 and $K_1'C_1'$. We take all differences between $M1$ and $M1'$ to be expressed by the imposed and incurred costs and $F_{M1}=F_{M1}'$. If the difference between $M1$ and $M1'$ is small enough $M2$ does not take notice, then imposed fitness $K_1=K_1'$. We now have three cases:

- a) If $C_1' < C_1$ then $M1'$ is unconditionally more fit, and is efficiently exclusive.
- b) If the conditions of (15) are met then $M1'$ is relatively fit while in competition with $M2$, but might decay out of the population if the competition ends.
- c) If the conditions of (15) are *not* met, then $M1'$ might still prevail if the $M1$ -type host population is partitioned and subject to group or kin selection, otherwise decaying.

Much seems familiar from the approaches to genetic evolution of altruism and selfishness. Points of view in the literature are summarized in a commentary by Sober and Wilson. [36] The importance here is not group or individual selection, nor is it meme selection exactly. It is a combination of meme propagation and selection as it interacts with individual and group selection.

In this section we weren't even concerned with altruism. It emerged when analyzing the evolution of exclusive memes, a consequence of the individual fitness burden of imposing exclusivity.

3.8 Arbitrary Group Formation (Splitting)

In the genetic theory of kin-altruism, differentiation of a population seems to be straightforward based on alleles. In behavioral transmission the line grows exceedingly thin. Referring to the preceding analysis of altruism, suppose a subgroup $M1''$ can be defined or imagined to already exist in part of the population. Let the meme $M1'$ be the idea that $M1''$ exists. By supposition the new meme $M1'$ spreads non-exclusively among most $M1$, but likely not among $M1''$. Substantively $M1''$ is the old $M1$, reduced in number. But $M1'$ must now be treated like a new $M2$ since it becomes exclusive of the fictitiously defined $M1''$.

By choosing the fictitious $M1''$ to be less than half of the population, the variant $M1'$ need only wait until it permeates most $M1$ not $M1''$, and then it has the advantage of $P_{M1'}/P_{M1''}$ being larger than one, and even if it has no imposed or incurred costs advantage it can arbitrarily increase its share of the population and is subject to positive natural selection.

Notice that by declaring $M1''$ to be an enemy population, $M1'$ gains the advantage of competitive altruism, effectively at the expense of $M1''$. So it is really a version of the old game of thieves turning against one another to increase their share. Unlimited repetition of this division is clearly deleterious to the overall population and likely several mechanisms have evolved to limit its repeated application, such as fairness.

Whereas group formation based on increased cooperation payoffs presumably tends toward formation of ever larger groups, group formation based on arbitrary mimetic differentiation tends toward group splitting. Consider hunter gatherers. Their groups will be small. Too large a group exhausts resources in the local region faster than the group can migrate. If the group becomes too large it needs to fission on some basis. Perhaps the $M1''$ may just leave voluntarily. If there is nowhere to go, a meme war either decreases fertility or directly reduces the population, bringing it back into equilibrium with its environment.

4. Discussion

4.1 Evolution of behavioral transmission of traits

Focusing on deleterious behaviorally transmitted traits produces such a dark view of them we should remind ourselves how little data we have on their evolution. Perhaps rationality does a good job of selecting useful traits, but then we have a hard time explaining climate change. While several species transmit cultural traits, the complexity of human culture is far greater, and all comparable species are extinct. We might be using data based on survivor bias.

Transmission outside of vertical culture and small group selection has only gradually come about in the last 5000 years. In interspecies or intergroup competition, lack of proficiency absorbing weapon, hunting or food technology may have led to extinctions, [32] and brought about the potential for lateral transmission of many less dramatic traits as groups consolidated for self-defense and post-agriculture economic cooperation, eliminating barriers to lateral transmission.

If some great joint goal such as equality, suppression of war, extension of life, or interstellar travel and colonization demands complete group unity and extreme sharing of high energy and high risk technology, it is possible to imagine a civilization either standing down from the activity or

inadvertently destroying itself. The math of our conclusions was not peculiar to humans and would apply to most species, making it a candidate explanation of the Fermi Paradox. [37-38] The energy of a starship traveling at a tiny fraction of light speed far exceeds any asteroid that ever struck Earth. And genetic engineering is likely necessary for some of these high-value goals.

Risk compensation theory holds that if a risky activity has utility, people accept the risk to a point. The quantitative version, crash rate theory, develops from evolutionary theory and holds that entities (people, corporations) must seek valuable features (behavioral traits) up to the point of diminishing return, or be competitively eliminated. As the process is stochastic and the deleterious aspect often delayed and sometimes amalgamated into a big event, there is not a smooth balance but large crashes (e.g. climate) which compensate large gains. [39]

4.2 What Kind of Replicator is a CRISPR Trait?

While a CRISPR edit of an embryo [40] takes N periods of time T to become an adult, and while the trait may be vertically inherited, this is not its primary spreading mode. Once accepted the trait will be introduced into a large number of embryos in a short time, effectively spreading laterally like a meme. The difference between memes and genes almost disappears in such circumstances. The equilibrium condition is (9) not (10). A negative reproductive fitness might be accepted for CRISPR edits that confer intelligence [41] or long life or other desirable personal attributes.

5. Conclusion

We have presented an analysis for deleterious behaviorally transmitted trait equilibrium which considers not only trait propagation but effects on host fitness and changes in host populations. The analysis was deliberately neutral with respect to the effect on genes, that is, the behaviors didn't favor one genotype over another, and so instead of emphasizing positive effects of co-evolution the negative effects of a competing second propagator were brought to the fore. Development of defensive mechanisms for longer lasting behavioral traits and resulting competitions and effects were analyzed in detail.

The analysis shows that such traits, if not restricted to propagate along with reproduction (vertically, in small cultural groups), are easily lodged permanently in a host species, infecting eventually all its members. These traits are not removed by natural selection unless confined to groups and group selection employed. They are cumulative and the accumulation of them poses an extinction risk.

We have seen how passive and active defenses might work. Some traits could forbid or antagonize other traits, and a great deal of social conflict might be traced to such defense if this point of view were taken in its analysis. Defensive memes themselves may pose extinction risk. Mutually exclusive memes are effective defenses, but only by affecting fitness. They also offer insight into mechanisms of inequality and altruism. Altruism emerges in the evolution of exclusive memes. In limited cases exclusivity can emerge on its own, but usually it is costly and requires altruism. In that case, it can emerge either as expected due to group selection or in one peculiar case if there is only meme competition.

The propagation of behaviorally transmitted traits independent of their hosts complicates feedback control of social phenomena. The accumulation of acceleration factors over decades or centuries further exacerbates intelligent management and may be connected to stuck states or long term cyclicity in society and its problems.

Our analysis has focused on longer term traits because it grew from an interest in altruism, group formation and conflict. Short term “memes” are more commonly analyzed in information and commercial sciences, where the ability to persuade or “convert” is assumed, and can be associated with information channel competition. We have shown conversion is less likely with long term traits, at least with deleterious ones where there is evolutionary incentive to evolve exclusivity. This might explain why spending on political ads is less effective, but we do not develop the idea. If proved true it would be very disappointing to those who believe dialog is the solution to ideological differences. Warring factions of altruists might be a more likely outcome.

These findings are more than a curiosity about altruism or inequality. With second replicators, we cannot depend on natural selection to eliminate our mistakes. Human rationality appears to have evolved to conceive effects occurring within one or two lifetimes. Economic overlapping generation models using realistic lifetime parameters work well at explaining real features of society such as economic growth rates and demographic transition (shift to low birth rates, especially with education of women). [42-43] The latter could be broadly interpreted as consistent with our thesis of the effect of behaviorally transmitted traits on fitness since any very long term benefits of a low birth rate and possibly declining population are not in the decision time horizon within the models. There is no retreat from civilization or technology desired or possible at our population levels. We suggest further empirical study.

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