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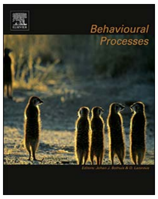

# Equifinality in empirical studies of cultural transmission

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## ABSTRACT

Cultural systems exhibit equifinal behavior – a single final state may be arrived at via different mechanisms and/or from different initial states. Potential for equifinality exists in all empirical studies of cultural transmission including controlled experiments, observational field research, and computational simulations. Acknowledging and anticipating the existence of equifinality is important in empirical studies of social learning and cultural evolution; it helps us understand the limitations of analytical approaches and can improve our ability to predict the dynamics of cultural transmission. Here, I illustrate and discuss examples of equifinality in studies of social learning, and how certain experimental designs might be prone to it. I then review examples of equifinality discussed in the social learning literature, namely the use of s-shaped diffusion curves to discern individual from social learning and operational definitions and analytical approaches used in studies of conformist transmission. While equifinality exists to some extent in all studies of social learning, I make suggestions for how to address instances of it, with an emphasis on using data simulation and methodological verification alongside modern statistical approaches that emphasize prediction and model comparison. In cases where evaluated learning mechanisms are equifinal due to non-methodological factors, I suggest that this is not always a problem if it helps us predict cultural change. In some cases, equifinal learning mechanisms might offer insight into how both individual learning, social learning strategies and other endogenous social factors might by important in structuring cultural dynamics and within- and between-group heterogeneity.

## 1. Introduction

Within evolutionary behavioral ecology and the human social sciences there is great interest in the conditions under which social learning is employed. Within social learning research, there is much effort directed toward understanding how and whom organisms learn from when given a variety of potential demonstrators to copy. These social learning strategies (Laland, 2004) or transmission biases (Boyd and Richerson, 1985; Henrich and McElreath, 2003) affect cultural dynamics and are important for understanding the adaptive significance of social learning in many organisms. These biases are also important facets of the accumulation of cultural traits which have enabled our own species to make a living in myriad ecosystems.

Since its inception, cultural evolution and social learning research has developed a rich body of quantitative theory inspired by other fields such as population biology, economics, and quantitative psychology (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). The conceptual grounding permitted by quantitative theory permits us to generate predictions for the conditions under which social learning (or particular social learning strategies) are likely to evolve as well as the short-term behavioral dynamics of different transmission biases or social learning strategies.

Empiricists have set out to test the predictions of social learning and cultural evolution theory in humans with experiments in controlled laboratory settings (McElreath et al., 2005, 2008; Rendell et al., 2010; Morgan and Laland, 2012), in the field (Kline et al., 2013; Berl and Hewlett, 2015; Reyes-García et al., 2016), and from historical records (Heinrich, 2004) and archaeological evidence (Crema et al., 2016). Similar investigations have been directed toward non-human animals as well (see Fragaszy and Perry, 2004; Hoppitt and Laland, 2013 for many examples). While much work has found evidence that supports the utilization of particular social learning strategies, discerning among particular social learning strategies can be challenging, particularly if organisms integrate personal and social information or use multiple strategies simultaneously (McElreath et al., 2008; Barrett et al., 2017).

In addition to identifying learning strategies, cultural dynamics may prove challenging to predict due to social factors (group fissions and fusions, rank) and demographic factors such as birth and death rates, changes in population size (Heinrich, 2004; Lake and Crema, 2015), and migration rates (Powell et al., 2009) which may structure cultural

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transmission independently of individual cognition. Simultaneously, new behaviors may be invented and/or disproportionately copied by different groups members over time (Perry et al., 2017; Aplin et al., 2017). Behaviors may also go extinct due to transmission biases or neutral effects such as drift (Boyd and Richerson, 1982).

These complexities and the dynamic nature of culture suggest that cultural systems are often constantly changing and affected by multiple phenomenon. To use terminology from general systems theory (von Bertalanffy, 1969), a cultural entity is an *open system* – its behavior is affected by the flow of external information, agents, and ecological processes into the system. Being open, cultural systems are unlikely to reach a final, stable equilibrium. The appearance of cultural stability (whether it is relatively unchanging foraging behaviors, religious beliefs, or technologies) is more likely to be a temporary steady state rather than a stable equilibrium. This, combined with the influence of multiple external factors, makes identifying the processes that shape cultural dynamics and transmission exceptionally challenging.

Being open, cultural systems are likely subject to *equifinality*. Equifinality is the possibility that in a dynamic, open system, the final observed state can be arrived at via different mechanisms and from different initial states (von Bertalanffy, 1950, 1969). The term was originally coined in developmental biology to describe the phenomenon of an embryo developing into morphologically indistinguishable juvenile organisms via multiple, experimentally manipulated, developmental pathways (Driesch, 1892). In the case of cultural transmission, equifinality might suggest that multiple learning mechanisms are equally likely to lead to the same observed final frequencies of socially learned behaviors. This identical final state (or steady state) may be reached from either identical or different initial frequencies. Additionally, cultural systems may also be subject to *multifinality*, where different final states may be arrived at from the same initial state via identical mechanisms. However, in this paper we will largely discuss instances of equifinality.

Equifinality occurs, to some extent, in all studies of cultural transmission. Its existence has been noted since the early days of gene-culture coevolution research (Lumsden and Wilson, 1980). The phenomenon we observe and measure in rigorously-controlled laboratory experiments, simulations, and observational studies are potentially caused by multiple mechanisms – most of which are unevaluated. Many of these mechanisms we are incapable of imagining or they might be unrealistic. However, iteratively combining theory and an understanding of the natural history of our study systems permits us to hypothesize and test different mechanisms that may give rise to the phenomenon we observe in our studies.

That there is an infinitely large strategy space populated by innumerable theoretical mechanisms which may create the patterns we observe in nature might seem daunting. It may drive many a young researcher to question (or nihilistically disavow) the entire scientific enterprise. However, science still permits us to learn about the world – even though we often err. We still increase our understanding of, and ability to predict, how culture is transmitted and affects the behavior of individuals and groups. This is because our theory is constrained, informed, and progressed by our understanding and curiosity about our study system's natural history.

Equifinality is unavoidable; but anticipating plausible instances of it can aid researchers in identifying better approximations of the “true” processes that affect cultural dynamics. Anticipating equifinality may also help us eliminate plausible alternative processes that might lead to the outcomes we observe in studies of social learning. In some instances equifinality may be addressed by modifying experimental design, analyzing the dynamics of learning, or explicitly linking individual-level cognitive processes to population-level behavioral variability.

In other cases, discerning between different learning strategies may not be possible. This is not always a problem, as it may suggest that there is some redundancy in the cognitive strategies used to acquire adaptive behavior and reach a steady cultural state – much like there are multiple developmental pathways to create a healthy organism. Equifinality might also hint that factors such as non-random assortment or individual variation in a population might be important factors in structuring the observed frequencies of cultural traits. Anticipating equifinality requires entertaining more plausible complementary or alternative hypotheses. This will make research programs more rigorous and offer more insight into cultural transmission.

Here, I illustrate examples of how equifinality may be partially addressed by: (1) varying the initial conditions of cultural traits in a study (when possible); (2) using analytical approaches that look beyond the initial and final states of cultural system and address behavioral dynamics; (3) modeling individual cognition and linking it to population level patterns. I also suggest ways that researchers might anticipate instances of equifinality and whether their methods or data permit them to adequately rule out alternative learning mechanisms.

## 2. A graphical example of equifinality between social learning strategies

Diffusion curves, which plot the changing frequencies of traits in a population as a function of time, may be used to illustrate simple examples of equifinality. Fig. 1 shows diffusion curves for two behaviors which differ in pay-offs plotted for 4 different commonly studied learning strategies (varied across rows) across a range of initial frequencies (varied across columns).

In this finite population ($n = 50$), there exists two behavioral variants, $A$ and $B$. At time $t = 1$, $A$ occurs in $x$ proportion of individuals and $B$ occurs in $1 - x$ proportion of individuals. A confers a pay-off, $\pi_A$, drawn from a truncated normal distribution of mean = 10 and standard deviation = 2, while $B$ confers a lower pay-off, $\pi_B$, with mean = 9 and standard deviation = 2. Simulations within a panel in Fig. 1 may differ after identical initial conditions due to drift in a finite population. Code for simulations and graphs can be found here: https://github.com/bjbarrett/equifinality2017.

I chose four commonly studied learning strategies out of an infinitely large learning strategy space. For the empiricist not well versed in mathematical models of social learning I explicitly specify them in the text below. I also link to R-code to reproduce Fig. 1 for the reader to explore and experiment with by varying parameter size or population values.

The four learning strategies are as follows (with reference to behavior $A$):

1. **Individual-reinforcement learning** takes on the form:

$$\Pr(A|\alpha,\lambda)_{t+1} = \frac{\exp(\lambda\alpha_{A,t+1})}{\exp(\lambda\alpha_{A,t+1}) + \exp(\lambda\alpha_{B,t+1})} \tag{1}$$

where

$$\alpha_{A,t+1} = \phi\pi_{A,t} + (1-\phi)\alpha_{A,t} \tag{2}$$

In Eq. (1) the probability of choosing behavior $A$ is conditional upon weights given to each behavioral choice ($\alpha$) at each timestep and sensitivity to individual payoffs ($\lambda$). $\alpha$ is updated at each timestep based on the most recently experienced pay-off ($\pi$) and memory of previous experiences weighted by $\phi$ in Eq. (2). This formulation of individual learning is similar to the Rescorla–Wagner rule (Rescorla and Wagner, 1972), and is one that is commonly used in studies of behavioral economics (Camerer and Hua Ho, 1999) and cultural evolution (McElreath et al., 2005, 2008). Here $\lambda = 1$ (choice is proportional to differences in payoffs) and $\phi = 0.25$ (weighing past experiences more heavily than recent ones). In this simulation, attraction scores, $\alpha$, were set to make individuals choose each behavior with the same initial probabilities listed in each column.

2. **Linear transmission** (also known as random copying or unbiased imitation), where the probability of acquiring a behavior is a function of its frequency in the population in the previous timestep:

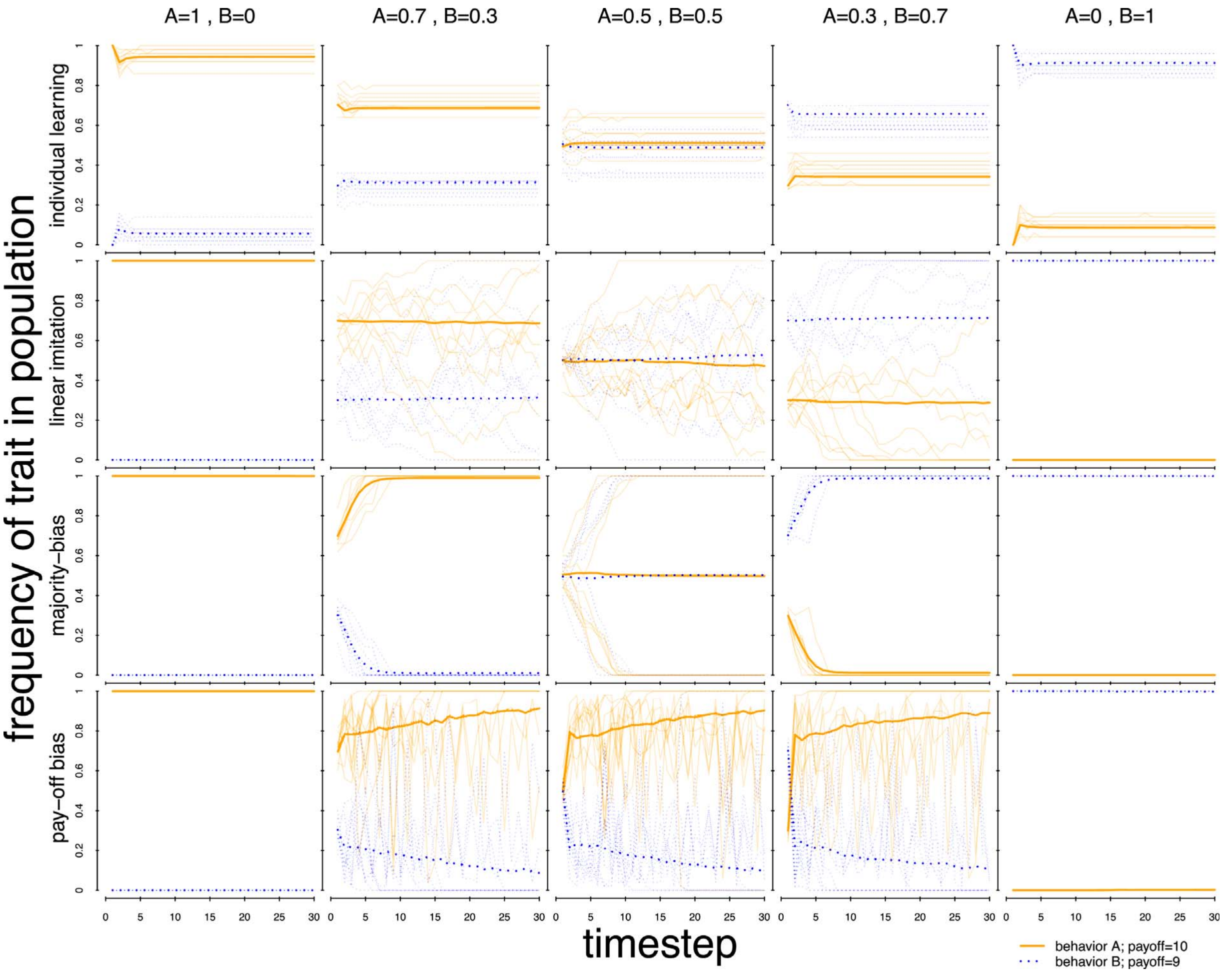


**Fig. 1.** Diffusion curves for 4 different learning strategies in a finite population ($N = 50$) over a range of initial conditions. Each row corresponds with a particular leaning strategy (labeled on the left side). Each column corresponds to the initial frequencies of each behavior in the population (labeled on top). Dark line is the average of 500 simulations for each strategy/initial conditions combination. Lighter lines are the dynamics of 10 random simulations to show the variation of dynamics each strategy may produce. Note: As population size increases, the influence of drift decreases; each random simulation is more likely to represent the mean of all simulations (akin to a nearly infinitely large population).

$$\Pr(A|A, B)_{t+1} = \frac{N_{A,t}}{N_{A,t} + N_{B,t}} \tag{3}$$

Here $N$ is the number of individuals in that population performing a particular behavior (denoted by subscripts) at timestep $t$.

3. **Majority-biased learning**, also known as positive frequency dependence, conformity-biased learning, or conformist transmission, where more common traits are disproportionately copied takes the following form (assuming $f > 1$):

$$\Pr(A|A, B)_{t+1} = \frac{N_{A,t}^{f}}{N_{A,t}^{f} + N_{B,t}^{f}} \tag{4}$$

Higher values of $f$ indicate a greater strength of majority bias. It is important to note that other mathematical formulations of this learning strategy exist that produce similar dynamics (see Henrich and Boyd, 1998; Kandler et al., 2017 for examples). If $f = 1$, Eq. (4) is identical to linear imitation in Eq. (3), whereas if it is $< 1$ we observe anti-conformist (or minority-biased) transmission. In this simulation, $f = 1.5$.

4. **Pay-off-biased learning** Here we show compare-means success bias (Baldini, 2013) where the observed behaviors of conspecifics with higher mean payoffs are disproportionately copied. It takes the following form:

$$\Pr(A|A, B)_{t+1} = \frac{\exp \beta \overline{P}_{A,t}}{\exp \beta \overline{P}_{A,t} + \exp \beta \overline{P}_{B,t}} \tag{5}$$

Here $\beta$ is the strength of pay-off bias, while $\overline{P}$ is the mean pay-off of a behavior ($\pi$ for an individual in Eq. (2)) averaged across all observed individuals at the designated timestep. For this simulation $\beta = 1.5$.

Within this four strategy space, I intentionally chose a limited parameter space which includes the specified initial frequency (and number) of cultural variants, population size, and chosen parameter values to highlight examples of equifinality. The reader may criticize these simulations and note that exploring the parameter space and changing specified values, looking at multiple points in the time series, or comparing the variance in dynamics that each learning strategy might address particular examples of equifinality (or introduce new ones). If you are such a reader – great! My intent is to encourage such thought exercises so that we might engage in them with our own research.

### *2.1. Equifinality due to lack of variance (i.e. fixation of a trait)*

One clear example of equifinality visible from diffusion curves is when one behavior is fixed in the population, as visualized in the first and last columns of Fig. 1. Ignoring the possibility of individual innovation, if individuals do not observe any variation in a trait in their new social environment, they only have one behavior from which to choose. This does not permit researchers to discern between individual learning, or the three proposed learning social learning strategies.

This "fixation limitation" has been a criticism (Van Leeuwen and Haun, 2013) of several studies showing evidence consistent with conformity in primates (Whiten et al., 2005; Dindo et al., 2009; van de Waal et al., 2013). If an individual copies the *only* observed behavior, individual learning, linear imitation, pay-off bias, and conformist-bias are all equally plausible mechanisms for social learning regardless of an individual's previous experience. It should be noted that this criticism has initiated fruitful discussion about methods and definitions in previous studies of conformity-biased learning in wild primates (see Van Leeuwen et al., 2016; Whiten and van de Waal, 2016).

Changing the range of initial frequencies of behavioral variants, as is varied across columns in Fig. 1, better permits finding evidence for particular learning strategies and eliminating plausible sources of equifinality. As learning strategies may produce different dynamics from different initial conditions, variation in the initial frequencies of behavior can improve inference and address particular causes of equifinality. For example if adaptive behavior is common (Fig. 1, column 2) majority-bias and pay-off bias can lead to the same outcome – the rarer, low pay-off behavior is eliminated while the higher pay-off behavior becomes more common. By varying the initial conditions and making adaptive behavior rare, we can reduce the likelihood of majority-bias/ conformist transmission as a plausible mechanism (but not always if weak conformist transmission is combined with individual reinforcement learning in a population with individual variation (Aplin et al., 2017).

### 2.2. *Comparing initial and final frequencies of a trait in a population*

Many studies of social learning compare the frequencies of traits at the initial and final stages of an experiment or the averages after an experimental treatment (Dindo et al., 2008; Pike et al., 2010; Pike and Laland, 2010; van de Waal et al., 2010). In observational studies the frequencies of traits at two points in time are compared after "natural experiments" such as development (Perry, 2009) or migration (van de Waal et al., 2013; Wrangham et al., 2016) to evaluate hypotheses about social learning. However, methodological approaches that compare two points from a diffusion curve or average frequencies across two stages of the transmission process are subject to analytical equifinality – the statistical methodologies used to identify learning mechanisms do not adequately discern among hypotheses. To illustrate, when the highest pay-off behavior is most common (Fig. 1 column 2, $A = 0.7$, $B = 0.3$), there are a range of conditions where the results are equifinal – the highest pay-off behavior may reach or approach fixation via pay-off bias, conformist bias, and linear imitation (in rare cases visualized by lighter lines from individual simulations). Similarly, linear imitation may give results consistent with conformist bias or anti-conformist bias (not graphed), and the chances of this occurring increases with smaller population size due to cultural drift. For linear imitation variation among dynamical trajectories of simulations illustrate multifinality due to drift in a small population.

Although comparing the initial and final frequencies of a trait in a population provides evidence consistent with particular social learning strategies, it greatly limits our ability to rule out other plausible mechanisms. It is therefore imperative to: (1) vary the initial frequencies of traits across experimental treatments, (2) look at multiple frequency distributions in the time series, (3) and/or use methodological approaches that explicitly model the temporal dynamics of behavior. 1 is more plausible in controlled experimental setups, while 2 or 3 are imperative in observational studies where control is lacking or limited.

## 3. Individual vs. social learning: equifinality in diffusion curves

Looking at Fig. 1, one may appreciate that a methodological approach which looks at the *dynamics* of learning over time can help us address particular instances of equifinality. While the dynamics of behaviors are always better evidence than single point estimates (Kandler et al., 2017), the dynamics of a behavior over time may also be misleading. This is well illustrated by the debate over whether sigmoidal diffusion curves are exclusively indicative of social versus individual learning, a topic which has been well reviewed by Reader (2004) and Hoppitt et al. (2010).

A sigmoidal, or S-shaped, diffusion curve is commonly seen across a wide range of the diffusion of technological innovations in human cultures (Rogers, 2010) and has been suggested to be evidence consistent with (Boyd and Richerson, 1985) or solely a product of biased cultural transmission (Roper, 1986; Henrich, 2001). The shape of the sigmoidal curve is argued to be the function of the relative proportion of culturally knowledgeable and naïve individuals in a population. At the beginning of a time series a system is likely to contain few or no innovators, and diffusion curves exhibit a approximately horizontal floor effect. As behavior spreads through the population the curve accelerates upward, begins to decelerate as fewer naA_ve individuals remain, and finally plateaus either due to a ceiling effect (reaching fixation in a population) or reaching a steady state where it is no longer transmitted to (or lost by) other members in the population. This is visible in examples of majority bias and pay-off bias in Fig. 1.

While sigmoidal diffusion curves are often produced by social learning, they are not always a signature of social transmission. Population structure (Laland and Kendal, 2003) and variation in latency among individual learners to solve a task (Lefebvre, 1995; Reader, 2004) can lead to sigmoidal curves under individual learning. Hoppitt et al. (2010) show that the individual learning of an n-sequence task, where n steps are required to successfully perform a task, can also lead to a sigmoidal curve if the rate of learning for each step is relatively stable or if individuals are reinforced for successfully solving each step. Additionally, if the neophobia of individuals toward engaging in a new task degrades over time, a sigmoidal pattern may be produced. While increasing reliance of social learning almost always leads to an increasingly S-shaped curve, the shapes of diffusion curves may not be reliably used to discern individual from social learning. More nuanced approaches of analysis that link the time series of behavior to social association patterns such as network based diffusion analyses (Franz and Nunn, 2009) are better tools, although some of these approaches' utility is constrained by task structure (Hoppitt et al., 2010) and the questions which researches are attempting to address (Hoppitt, 2010).

## 4. Equifinality in analyses of conformity-biased learning

Conformity-biased learning (also known as majority-biased learning, conformist transmission, and positive frequency-dependent learning) is the propensity to preferentially copy the most frequent trait in a population. It has likely received more theoretical and empirical attention than any other social learning strategy across taxa. Conformity-biased learning may act as an efficient shortcut to acquiring adaptive behavior in spatially heterogeneous environments (Boyd and Richerson, 1985; Nakahashi et al., 2012), may enforce norms of punishment and promote cooperative behavior (Henrich and Boyd, 2001) and may decrease within- and increase between- group heterogeneity providing conditions upon which cultural multi-level selection may act (Boyd and Richerson, 1982, 1990; Henrich and Boyd, 1998; Richerson et al., 2016). Interestingly, it can also lead to maladaptive behavior if what the majority is doing is not the best option and individuals ignore or lack personal information, or if environments change temporally (Nakahashi et al., 2012; Whitehead and Richerson, 2009).

### 4.1. *Equifinality among different varieties of positive frequency dependent learning*

Experiments have found evidence consistent with conformity-biased learning in humans (Efferson et al., 2008; Morgan and Laland, 2012; Muthukrishna et al., 2016) and non-human animals in captive (Whiten et al., 2005; Dindo et al., 2009; Chou and Richerson, 1992) and wild contexts (van de Waal et al., 2013; Aplin et al., 2015b). However, there has been much debate about whether many of these experiments actually display conformity, as experimental designs or the lack of alternative evaluated hypotheses (Van Leeuwen and Haun, 2013) limit inferential power.

The topic of conformity-biased learning is differently defined and interpreted by many scholars (see Claidière and Whiten, 2012; Van Leeuwen et al., 2016; Aplin et al., 2015a for discussions on differential uses and definitions of "conformity" relevant to this debate). Following Asch (1956), the social psychology tradition suggests that individuals must abandon personal experience and follow the majority to constitute "conformity," while the cultural evolution literature typically defines "conformist transmission" or "majority-biased learning" as when naïve individuals copy the most common trait, and are subject to a majority influence. However there is much interchangeable use between these terms as people come from different disciplinary backgrounds and may not be familiar with terminology in each other's subfield. Perhaps it is simply a product of conformity being a terser way of describing "conformity-biased transmission" or "positive frequency-dependent learning" when trying to meet character limits for publication. Issues arising from verbal looseness might be better solved by explicitly stating (perhaps in mathematical form) what definitions of "conformity" we intend to use – especially if we believe the distinction between operational definitions of positive frequency-dependent learning to be important.

Two recent experimental studies have found evidence consistent with conformity-biased learning in free ranging and wild populations of primates (van de Waal et al., 2013) and song birds (Aplin et al., 2015b). van de Waal et al. (2013) exposed vervet monkeys, *Chlorocebus aethiops*, to two colors of corn (red and blue), one of which was made bitter with aloe. This trained vervets to prefer the non-bitter color. When individuals migrated to a different group (trained on the opposite color) they switched from their previous color preference to the one which was used most commonly in their new group (with the exception of some low-ranking individuals). These preferences persisted after group fissions (van de Waal et al., 2017).

Aplin et al. (2015b) utilized a controlled, and replicated experimental design where demonstrator great tits, *Parus major*, were trained in captivity to access mealworms in automated feeders by two methods: (1) sliding the blue side of a feeder door to the right or (2) the red side to the left. Control birds were trained to open neither side of the door. Their experiment found that subgroups in the treatment groups which observed trained demonstrators showed a strong bias for copying the original seeded technique of the demonstrator and acquired behavior rapidly (approximately 20 days). Control birds took longer to solve the task, and the birds in that population showed no strong preference for either technique. Network-based diffusion analyses showed strong evidence for social over individual learning. Additionally, the acquisition curve, a plot of the probability of adoption vs. frequency in the group, showed a sigmoidal curve indicating a bias toward common behaviors and aversion to rare ones. This bias towards the more commonly observed behaviors existed for over a year.

Aplin et al. (2015b) and van de Waal et al. (2013) were critiqued for operationalizing conformist transmission as "copying the majority of behaviors" as opposed to "copying the majority of individuals." With regard to Aplin et al.'s study, van Leeuwen et al. (2015) accepted that their population-level patterns were consistent with conformist transmission, but critiqued their individual level results with regard to whether *individuals* were being conformist. van Leeuwen et al. argued that analysis should focus on the level of the individual, as that is more in line with the original formulation in the social psychology literature (Asch, 1956) and is more aligned with the potential advantage for a primary advantage of conformity – drawing wisdom from the crowd.

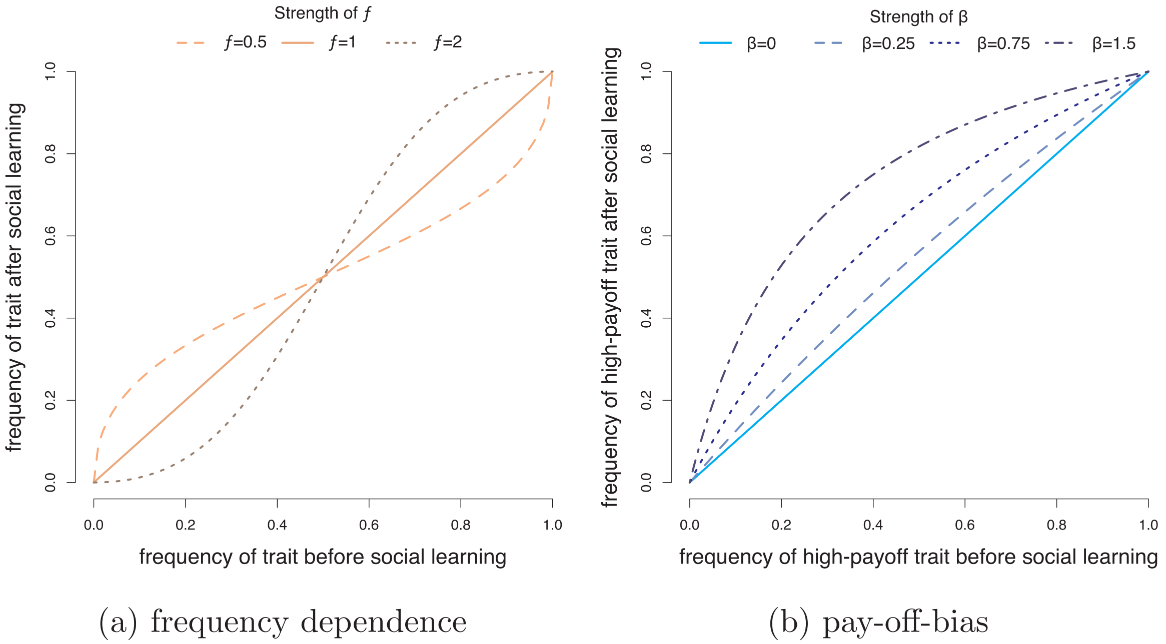
While there are distinct advantages to linking individual level analysis to population level dynamics (to be discussed in Section 6), frequency dependent learning strategies that attend to either frequency of behaviors in a population or the frequency of individuals are often equifinal (Aplin et al., 2015a; Whiten and van de Waal, 2016). While van Leeuwen et al. (2015) acknowledge this, they dwell on instances where this is not the case. Mathematical models of all types of frequency-dependent social learning are often agnostic and highly variable about their word choice regarding whether individuals are copying behaviors, individuals, or traits (Aplin et al., 2015a). In most theory, the units by which one may count conformity are functionally equivalent. In Aplin et al.'s great tit data, they found evidence for a strong majority-bias when counting either individuals or behaviors (Aplin et al., 2015a) – both definitions were equifinal.

However, there might be good reasons to think that counting behaviors may be more plausible than counting individuals. For many organisms, there may be increased cognitive load for bookkeeping what is the most common behavior among individuals in a population and the "counting individuals" definition is dependent on other cognitive assumptions of how animals monitor their social groups. Unlike most learning experiments, animals often must choose from more than 2 behaviors in nature. Keeping track of a dynamic time series of 5–10 (or more) behaviors, remembering which were the most commonly observed (ignoring sampling error), and integrating that information across a potentially large population is likely cognitively demanding. The cognitive demands associated with keeping tabs of what individual's do, especially in a large population, might lend themselves to a more efficient type of majority bias learning such as copying the most commonly observed trait or a "rule of 3's" – sampling three individuals in the population and copying what is most common (Boyd and Richerson, 1985; Acerbi et al., 2016). An understanding of the perceived cognitive capacities, social dynamics, and group sizes of our study systems can inform if there might be reason to distinguish between counting behaviors or individuals or if that distinction does not matter.

Perhaps, it might be better to think of conformist transmission or majority-bias as a family of different types of majority influence. One reason is that our mathematical models of conformity, while useful, are not intended to precisely express all aspects of what goes on in reality. As mentioned earlier, there are multiple ways to express majority influence, as testified by the existence of multiple mathematical formulations portraying an identically named mechanism. Models generate predictions for how systems behave to test empirically and act as a logical exercise to clarify our reasoning. Models of conformity are recursive, and the social influence used to inform behavior at $timestep = t$ is solely function of what was observed in others at $timestep = t - 1$. In reality, animals likely have some memory of the social information they have observed which is not accounted for in most models. The dynamics generated by "rule of 3-s," copying the majority of individuals, and copying the majority of behaviors are often equifinal and they all have to deal with some aspect of majority influence. Sometimes distinguishing between these equifinal mechanisms may not matter.

If we have a reason a priori to expect that distinguishing between multiple types of majority influence should matter, the necessity of these distinctions should be made clear. For instances where there are strong biases towards particular individuals (thus making copying the number of behaviors multifinal from copying individuals), we might expect that certain model biases (i.e. copy older or similar individuals) are operating, and these hypotheses should be evaluated alongside proposed examples of majority influence.

Using a similar family classification of learning strategies has been useful in understanding the varieties of success-biased learning. Individuals may copy the most successful behavior on average, also known as compare-means success bias (Baldini, 2013) or pay-off-bias (McElreath et al., 2008; Barrett et al., 2017) learning. Of these varieties of payoff-bias learning, behaviors may be copied proportional to their pay-offs (Kendal et al., 2009) or there may be a strong bias towards higher pay-off behaviors (McElreath et al., 2008). Another potential success-biased learning strategy is to "imitate the best" *individual* in a



(a) frequency dependence

(b) pay-off-bias

**Fig. 2.** Instantaneous evolutionary dynamics of (a) frequency dependent and (b) pay-off biased learning. Panel a shows 3 types of frequency dependent learning: anti-conformist ($f = 0.5$), linear ($f = 1$), and conformist ($f = 2$) transmission. *Y*-axis is the average frequency of trait after social learning. *X*-axis on panel a shows frequency of trait before social learning. Panel b shows 3 strengths of pay-off bias: ($\beta = 0, 0.25, 0.75, 1.5$). *Y*-axis is the average frequency of high pay-off trait after social learning and *X*-axis shows frequency of higher pay-off trait before social learning. High pay-off behaviors yield 10 units of fitness, low pay-off behaviors yield 9. Note that solid lines on both panels where (a) $f = 1$ and (b) $\beta = 0$ are equivalent to random choice.

population (Baldini, 2013). There are cases where this distinction matters. Compare means success-bias performs better when behaviors are rare (Baldini, 2013, 2012), whereas "imitate the best" can under perform when lower pay-off behaviors occasionally yield a high payoff due to stochasticity. However, under many conditions these learning strategies are likely equifinal, especially when a novel, high-payoff behavior is introduced by a single individual in a population. We can learn much by comparing the cases where differentiating these strategies matters (see Lake and Crema, 2015 for a discussion of this topic).

## 5. Population-level dynamics and acquisition curves

Analyses that address the dynamics of the learning process are essential for making good inferences about social learning strategies and to avoid problems associated with equifinality. Plotting instantaneous dynamics of cultural transmission (McElreath et al., 2008), also known as acquisition curves, can be an informative way of understanding how changes at the population level are a function of the social cues that inform learning. Acquisition curves plot the probability of acquiring a trait as a function of a changing range of cues used for social learning.

Frequency-dependent learning (Fig. 2a) is comprised of three different learning strategies: anti-conformist, linear, and conformist transmission. Linear transmission, also known as random copying (where $f = 1$ in Fig. 2a; Eq. (3)) yields a linear acquisition curve. Negative-frequency dependence generates a mirrored-sigmoid – where less common behaviors show an increased probability of adoption and less common behaviors yield a lower probability of adoption. Conformity-biased learning yields a sigmoidal, or s-shaped, acquisition curve where more frequent traits are more likely to be copied, and rarer traits are less likely to be copied relative to their abundance in a population. Pay-off-biased learning acquisition curves plot the probability of acquiring the higher pay-off behavior after social learning. This generates a concave down curve where higher pay-off behaviors are more likely to be copied as a function of the strength of pay-off bias and the mean difference between pay-offs (Fig. 2b).

Aplin et al. (2015b) found that across treatments a sigmoidal acquisition curve predicted their data better that an acquisition curve consistent with linear imitation. Recently, the validity of these claims has been challenged by simulations (Van Leeuwen et al., 2016) and agent based models (Acerbi et al., 2016) suggesting that multiple, other unevaluated learning strategies could give rise to a sigmoidal acquisition curve – they are subject to equifinality. These proposed processes included showing a bias for a variant preference (as Smaldino et al., 2017 points out is equivalent to Boyd and Richerson's 1985 "direct bias"), copying a subgroup of demonstrators, or counting behaviors instead of individuals (Acerbi et al., 2016). Smaldino et al. (2017) suggest that many of these claims were not robust or are products of a limited range of experimental conditions that are unlikely to exist in the real world. While copying a subgroup can generate a sigmoidal curve under a limited range of conditions (including small population size), many of these scenarios such as monopolization by a single individual or subgroup of individuals, they argue, are likely to be noticed and accounted for by an empiricist observing organisms interacting.

The claim that conformity cannot be identified from population signatures simply because other learning mechanisms may generate a sigmoidal acquisition curve is an exceptionally strong one. If rigid adherence to unifinality, which may only appear in closed systems such as basic chemical reactions and classical mechanics, is applied to any study of cultural transmission we would be unable to make any progress about understanding how organisms learn or culture affects behavior and evolution. However, hypothesizing alternative mechanisms that may generate patterns consistent with our hypothesized social learning strategies should be commended and performed more by empiricists studying social learning. However, natural history and relevant theory should inform the alternative mechanisms we evaluate. Infinite social learning mechanisms likely exist which are affected by multiple endogenous and exogenous factors. There likely exists additional processes that generate the patterns we observe in cultural systems – even if it not the "true" data generating process.

## 6. Limits of population level dynamics for making inferences about individual processes

While Smaldino et al. (2017) convincingly argue that sigmoidal acquisition curves provide solid evidence for conformist transmission in most experimental scenarios, a degree of caution should still be made about using population-level signatures of social learning to make inferences about how individuals learn. If individuals use multiple learning strategies, combine individual and social learning, differ in when and whom they direct attention toward, or vary due to individual differences associated with age or population structure (Barrett et al., 2017; Kandler et al., 2017; Aplin et al., 2017), population-level signatures may be misleading. Cultural dynamics emerge from the interplay between individual cognition and what is available to copy in a population at any given time. For this reason, approaches that link the behavior of individuals (the level at which the hypothesized psychological mechanisms of learning operate) to population level signatures are of great utility. One example of this can be seen in models that use hierarchical experienced weighted attraction models that explicitly account for individual differences. Barrett et al. (2017) and Aplin et al. (2017) both show that individuals in a population display different acquisition curves as they learn differently and/or access different social and personal information. These models also generate individual level predictions which may be plotted against raw data. In a study of social learning of extractive foraging behaviors in capuchin monkeys, population-level diffusion curves (Fig. S3) did not describe the frequency or timing of behavior acquisition for almost all individuals in the population (Barrett et al., 2017).

A recent simulation (Kandler et al., 2017) evaluated the interplay between age structure and transmission mechanisms to evaluate the limitations of population-level signatures in making inference about the social learning strategies employed by individuals. Looking at a population where behaviors conferred no fitness benefit, Kandler et al. (2017) evaluated five social learning strategies. They found a range of scenarios where learning strategies could not easily be distinguished based on statistics alone, such as when potential for cultural change is low or population size is small. Interestingly, conformist transmission was typically easier to discern from other learning strategies, particularly in non-age-structured populations. Oblique and horizontal transmission could not be easily differentiated unless mutation rates were high and the bias toward oblique transmission was strong. Knowing the limitations of analytical approaches from simulations where data is simpler than what we collect in empirical studies is useful for understanding when results might be equifinal. If we choose to use population level signatures to make inference about individual processes it is important to explore the conditions where our inference might be limited.

## 7. Equifinality and non-random assortment

Another potential source of equifinality which warrants further exploration is how social relationships (Coussi-Korbel and Fragaszy, 1995) and social systems affect the probability of interacting before learning occurs. Empirical studies and models often assume that organisms are panmictic, or randomly interact with other individuals in a population. This is likely never the case. Assortment before learning may be equally as important as the psychological mechanisms in structuring cultural variability, and sometimes the two may not be able to be distinguished. This assortment may be an adaptive heuristic, such as deciding to bias attention towards kin or knowledgeable individuals. Other times it may be an indirect consequence of social behavior, such as avoidance of potentially dangerous demonstrator. Organisms may give the appearance of using particular social learning strategies, but in reality social factors may just structure whom they learn from independent of cognition. For example, in orangutans juvenile males will readily observe older females who are processing food, thus providing many opportunities for social learning. As males approach reproductive age, females will actively avoid them to avoid non-consensual matings – a common reproductive tactic in the unfrilled male orangutan morphotype (Russon, 2002). If animals disproportionately interact with kin or age-mates, it may be challenging to discern if they are randomly imitating whom they associate with or if they are seeking individuals out as sources of social information. Oftentimes, this distinction may not matter. But when organisms transfer to novel social settings or we wish to use social learning in applied contexts (i.e. animals in captivity being trained to acquire skills via social learning for wildlife reintroduction), making this distinction might be important.

## 8. Recommendations for addressing equifinality in cultural systems

Below I suggest several ways for researchers of social learning to begin to account for equifinality. It is not exhaustive, and may not be feasible for all researchers, but striving for some of these aims will hopefully improve our research programs.

### *8.1. Acknowledge potential for equifinality in your study system*

Equifinality is prevalent in studies of cultural transmission regardless of the quality of experimental design or ecological relevance of a study system. Culture is a dynamic process of interacting agents whose behaviors and beliefs change over time in response to changing demographic and ecological processes. It is inevitable that other unevaluated learning mechanisms may cause the patterns we see in our studies whether they be observational studies or controlled experiments. However, instead of ignoring or being fearful of equifinality, it is best to try and anticipate potential and probable causes. Failing to eliminate alternative hypotheses is not a failure when hypotheses cannot be discerned. Exploring or showing the conditions where hypotheses cannot be differentiated, openly communicating uncertainty, and improving our ability to predict cultural variability and dynamics is a ideal for which researchers should aim.

### *8.2. Evaluate multiple hypotheses informed by natural history*

Studies cannot begin to address equifinality unless multiple hypotheses are evaluated. It important to not merely look for evidence of social learning versus individual learning or conformity versus not-conformity (Van Leeuwen and Haun, 2013). However, these hypotheses should be informed by the natural history of the organisms we are studying and previous theory. If organisms have important kin-structure in their social system or frequently interact with sub-groups (i.e. school children interacting with age-mates in class), strategies like kin-biased and age-similarity-biased learning should be closely examined as they may be equifinal with other learning strategies. If organisms are long lived and have important age-structured differences in a population, evaluating learning strategies such as horizontal or oblique transmission might be important. For example, in white-faced capuchin monkeys pay-off biased social learning combined with individual reinforcement best predicts the diffusion of one extractive foraging tradition where behaviors differed in efficiency and efficacy. While being the best supported learning strategy in predicting behavior, pay-off bias exhibits a degree of equifinality with both negative frequency-dependence and age-biased learning as the highest pay-off behavior was initially the rarest and older individuals were more often more successful (Barrett et al., 2017). Statistical approaches that evaluate the relative joint contributions of multiple learning strategies and generate predictions to compare to data (McElreath et al., 2008; Barrett et al., 2017) can be helpful in identifying potential cases of equifinality or if organisms might be integrating multiple learning strategies simultaneously. As researchers move away from null-hypothesis significance testing towards approaches such as dynamic prediction-generating models and model comparison using information criteria, we will better be able to identify and explain instances of equifinality.

### 8.3. Simulate hypothesized generating processes and test methods

Equifinality may sometimes be due to constraints on analytical techniques, and sometimes these constraints are not apparent until these methodological approaches have been employed for some time in the literature. Using different approaches, it may be impossible to discern between different proposed learning mechanisms as is the case with sigmoidal diffusion curves and potentially in rare circumstances for sigmoidal acquisition curves (Acerbi et al., 2016) (but see Smaldino et al., 2017 for why this may not likely the case).

Simulating the hypothesized data generating processes and evaluating if and when one's statistical approaches can accurately rule out alternative hypotheses is an invaluable approach to inference. If we cannot identify a single well supported hypothesis, it may teach us something interesting about statistical methodologies and/or our study system that might have been not previously apparent. Data simulation and verification is important in studies testing the importance of newer statistical methodologies such as network-based diffusion analyses (Franz and Nunn, 2009; Hoppitt et al., 2010; Whalen and Hoppitt, 2016), experience weighted attraction models (McElreath et al., 2008; Kendal et al., 2015; Barrett et al., 2017; Aplin et al., 2017), or applied Bayesian computation (Kandler and Powell, 2015) as it teaches us about the effectiveness of our techniques and teaches us to be cautious for when they fail. For example, simulation and verification showed that TADA (time of acquisition diffusion analysis) is vulnerable to false positives when processes such as neophobia and subgoal learning are involved, leading to improvements upon methodological approaches (Hoppitt et al., 2010). Making data simulation and verification and code sharing a more standard practice in evaluating the effectiveness of social learning will make our studies more thorough and help address solvable issues of methodological equifinality.

#### 8.3.1. Contributions of quantitative archeology to addressing equifinality

Of the fields studying cultural transmission, quantitative archeology has perhaps been most attuned to equifinality (Premo, 2010; Kandler and Powell, 2015; Gerbault et al., 2014). Empiricists studying cultural transmission in current human and animal societies could learn much from their practices. Quantitative archaeologists have relied heavily on simulation to understand limitations on making inferences about cultural transmission (Crema et al., 2016). Archaeological assemblages often only provide researchers with the endpoint of a cultural process or snapshots of the frequencies of technologies across a time scale where change can happen quickly. Fine grained temporal data is rarely, if ever, available. Thus, some quantitative archaeologists emphasize the importance of remaining cautious about interpretation and use approaches such data simulation and verification to see what, if any, conclusions may be made (Kandler and Powell, 2015; Crema et al., 2016; Kandler et al., 2017).

Simulation in archeology has uncovered many examples of equifinality in their systems. Rorabaugh (2014) explored the effects of limited population size and bottlenecks on inferring about social learning strategies from the archaeological record using agent-based simulations. They showed that vertical transmission with drift and unbiased transmission (i.e. linear copying) are equifinal in limited population sizes, and that conformist transmission and prestige-bias are equifinal if prestigious indicators are only present in less that five percent of the population. After a population bottleneck, unbiased transmission and prestige-bias cannot be adequately discerned. Crema et al. (2014) used approximate Bayesian computation to show that anti-conformist transmission and unbiased transmission provide equally plausible explanatory models for data from Neolithic armature assemblages due to equifinality. Crema et al. (2016) showed that a fixed model of cultural transmission fails to describe changes in decorative motifs on Merzbach ceramic assemblages, and models which account for temporal changes in the types of cultural transmission (in this particular case, switches between conformist and anti-conformist transmission) that occur over time that do not assume equilibrium are essential for predicting the patterns observed in data. Their approach also suggests the importance for model selection approaches to data analysis used to infer plausible social learning strategies over antiquated approaches such as null-hypothesis testing.

### 8.4. Collect and analyze data

Data about cultural transmission should be analyzed with the originally proposed, simulated, and verified methods. Ideally, this should occur prior to data collection so researchers may refine experimental design. However, for historical datasets or long-term research projects methodological verification likely will occur after collection but before analysis. If analytical methods need to be changed, simulation and verification should be re-performed and the reasons for these changes should be communicated. Additionally, reporting results of models evaluating all alternative hypotheses will also make our results more robust and show that we cautiously entertained alternative and complementary hypotheses. Preregistration of studies under an open science framework (https://cos.io/), and open sharing of data and code in public repositories, makes it easier to achieve many of these goals and increases the probability of publication if our findings are highly equifinal or non-novel in a well-designed study (McKiernan et al., 2016).

If results show that we are unable to adequately discern between mechanisms, or that multiple learning strategies are equally plausible, that should not be viewed as a failure. Sometimes available quality and quantity of data may limit us from making strong (and more likely to be incorrect) inferences. Other times, unaccounted for factors such as age-structure (Kandler and Powell, 2015), bottlenecks (Rorabaugh, 2014), or drift in a population may make discerning between alternative learning strategies implausible. Other times equifinality is an inherent part of our study systems especially when we take into account that organisms bias whom they direct attention toward in addition to how they use information.

### 8.5. Communicate findings with care

In a world of infinite hypothetical mechanisms of cultural transmission, there is almost certainly an unaccounted for learning strategy that is equifinal with the ones we propose a priori. Instead of making definitive statements such as “organism x is conformist” we should instead communicate that our findings are “consistent with kin-biased learning” or we found “evidence for conformity-biased learning compared to the following alternative evaluated hypotheses.”

## 9. Conclusions

Equifinality is inevitable in studies of cultural transmission. Being aware of its potential will make our findings more rigorous, and in some cases may open up unanticipated avenues of inquiry for studying social learning and cultural evolution. Early approaches to science were heavily influenced by eliminating alternative hypotheses in simple, closed systems (von Bertalanffy, 1969). This is rarely an adequate option in the biological and social sciences. As the complexity of the systems we study grows and our experimental control decreases (or illusion of control disappears), we need to be more open to the possibility that the phenomena we observe in nature are likely caused by many processes. Anticipating, and pointing out potential for equifinality in studies of cultural transmission will help us point out the limitations of our inference or the complexity and nuance of our study systems. Science progresses because future scientists tell us we are always wrong (or at least never 100% right), despite how history revises the narratives of the uncertainty behind the process of scientific discovery (Kuhn, 1962). If we anticipate the cases where equifinality occurs, incentivize being careful and pointing out these limitations, our understanding of the complexities of cultural transmission will accelerate. At least, we will be wrong less often.

## Conflict of interest

The author declares no conflicts of interest.

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