Conformity in mate choice, the overlooked social component of animal and human culture

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# ABSTRACT

Although the role of conformity as a major driver for human cultural evolution is a well-accepted and intensely studied phenomenon, its importance for animal culture was largely overlooked until recently. This limited for decades the possibility of studying the roots of human culture. Here, we provide a historical review of the study of conformity in both humans and animals. We identify gaps in knowledge and propose an evolutionary route towards the sophisticated cultural processes that characterize humanity. A landmark in the study of conformity is Solomon Asch's famous experiment in humans in 1955. Contrastingly, the interest in conformity among evolutionary biologists has only become salient since the turn of the new millennium. A striking result of our review is that, although studies of conformity examined many biological contexts, only one of them looked at mate choice. This is surprising because the context of mate choice is probably the only one in which conformity has self-reinforcing advantages over generations. In effect, within a metapopulation, i.e., a group of subpopulations connected by individuals dispersing among them, dispersers able to conform to the local preference for a given type of mate have a strong and multigenerational fitness advantage. This is because as soon as females within one subpopulation locally show a bias for one type of males, immigrant females who do not conform to the local trend have sons, grandsons, etc. of the non-preferred phenotype, which negatively and cumulatively affects fitness over generations, in a process that is reminiscent of the Fisher runaway process. This led us to suggest a sex-driven origin of conformity, indicating a possible evolutionary route towards animal and human culture that is rooted in the social constraints acting on mating preferences within a metapopulation. In a generic model, we show that dispersal among subpopulations within a metapopulation can maintain independent Fisher runaway processes within subpopulations, while favouring the evolution of social learning and conformity at the metapopulation scale, both being essential for the evolution of long-lasting local traditions. The proposed evolutionary route to social learning, conformity, and all its cultural consequences, casts surprising light on one of the major processes that has participated in making us human; everything might have originated in sex. This would imply that all our fantastic cultural skills, and exquisite arts, religions, common beliefs etc., may have originated as a consequence of the basic and unavoidable importance of finding a mate that is optimal in view of the local conditions. We further highlight several research avenues to better define the spectrum of conformity, and to account for its complexity. First future studies of conformity should incorporate the experimental manipulation of group majority. We also encourage the study of the potential links between conformity and animal aggregations, collective actions and mate copying. Moreover, the validation of the sex-driven origin of conformity will rest on the capacity of human and evolutionary sciences to work jointly on the study of the origin of social learning and conformity. This constitutes a stimulating common agenda for these two domains and militates for a rapprochement between these two currently largely independent research areas.

**Keywords:** cultural evolution, conformity in humans, conformity in animals, sexual selection, mate choice, Fisher Runaway Process

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# INTRODUCTION

Cultural processes have played a major role in the evolution of humanity, and they still do. A central process of cultural evolution is social learning, which is a form of learning that specifically uses information obtained from another animal or its product to gain information about the environment (definition adapted from Heyes, 1994). Thus, social learning involves a wide variety of information channels and acquisition mechanisms (e.g., vision, hearing, olfaction) involving information processing mechanisms that are deployed in a social context to ultimately shape the learner’s behavioural traits (Danchin *et al.,* 2004). Social learning has been recognized as a crucial learning process for the transmission and spread of adaptive behaviours within and among populations (Laland, 2004; Rendell *et al.*, 2011; Aplin *et al.*, 2015).

A major characteristic of social learning for the establishment of cultural traditions and social norms in humans is conformity (Boyd & Richerson, 1985; Henrich & Boyd, 1998). There are several definitions of conformity or conformist bias used in the literature depending on the field. They range from “copy the majority”, which is a simple positive frequency-dependent bias (e.g., Laland, 2004) to “Aschian conformity”, where personal knowledge or preference is overridden by countervailing options performed by others (Asch, 1955). Perhaps the most popular and widespread definition of conformist bias or conformist transmission is defined as the *disproportionately likely* adoption of the most common variant within the local population (Boyd & Richerson, 1985). In effect, conformity can generate socially learned traditions that are both resistant to erosion and robust to invasion of alternative variants, potentially persisting over generations. Conformity can be responsible for a combination of within-group homogeneity and between-group heterogeneity.

Because of its central role for the emergence and maintenance of culture, conformity has long been a major topic of research in human sciences (Boyd & Richerson, 1985; Aoki, Lehmann & Feldman, 2011; Merrell, 2011; Claidière & Whiten, 2012; Efferson *et al*., 2016; Denton et al. 2020). Contrastingly, conformity became a major topic in evolutionary sciences only recently (e.g., Banerjee, 1992; Bernheim, 1994; Whiten *et al.*, 2005; Aplin *et al.*, 2015; van Leeuwen *et al.*, 2015; Danchin *et al.*, 2018), and a synthesis between these two scientific domains is still lacking. Here, we review the literature on conformity in both humans and animals, which have a lot in common but often receive little mutual attention. This review allows us to identify gaps in knowledge and suggest a general model for the evolution of social learning and conformity. Our review further suggests that conformity in mate choice deserves closer attention as sexual selection is a strong evolutionary force that has been largely overlooked up to now in this context. We aim to inspire new research agendas in both human and evolutionary sciences to determine in which context, e.g., mate choice or foraging, the cognitive processes that underpin the evolution of animal and human culture could have evolved and how they interact.

# II. EARLY DEFINITIONS: CONFORMITY OR POSITIVE FREQUENCY DEPENDENT LEARNING?

Before Boyd & Richerson (1985) coined their precise definition featuring an “exaggerated tendency” to adopt a majority behaviour, conformity was mostly a catchall word encompassing any individual tendency to adopt the majority behaviour. This has led to a lot of confusion around the very use of the word conformity across disciplines, even today (see Efferson *et al*., 2008 for a discussion). In this section, we propose a brief history of the term pre-dating Boyd & Richerson’s contribution of conformist bias. Most uses of the term conformity over this period would now be more accurately labelled as positive frequency-dependent social learning.

The influence of groups on individual behaviour first attracted attention in the early twentieth century (Jennesse, 1932; Sherif, 1935), but it was Solomon Asch (1955) who popularized the term *conformity* itself. Using a simple ‘visual judgement’ task, Asch documented that people were willing to abandon their own personal preferences (or convictions) when confronted with a disagreeing majority opinion. He ascribed this behaviour to social pressure and called this innate tendency to self-align on group opinion 'conformity’. Asch’s findings became momentous in developing the field of social psychology. They were replicated many times across different age classes and cultures, while varying other factors such as group size, motivation, task difficulty or relevance (Baron, Vandello & Brunsman, 1996; Bond, 1996; Bond & Smith, 2005; Griskevicius *et al.*, 2006). Later, Latané’s (1981) work on ‘social impact theory’ provided a tentative conceptual framework for these findings. Drawing a parallel with physics, Latané pictured social influence as a force emanating from, and acting on individuals (e.g., peer pressure). The intensity of this force could depend on the source group’s size, its behavioural composition (the proportion of individuals performing the various behaviours), its status (such as prestige), or its proximity in time and space to the target individual (see also Latané & Wolf, 1981). Overall, social psychology had suggested a proximate reason for ‘conforming’, namely that people inherently dislike going against the majority.

Note that these early works equated conformity with a linear increase of the likelihood to adopt a behaviour as that behaviour becomes more common in the population – what today is called positive frequency-dependent social learning. Conformist bias as defined by Boyd & Richerson is actually a particular case from this class of learning rules (adoption of the most common variant needs to be disproportionately likely). Still, debates from this early period may provide useful insights regarding positive frequency-dependent social learning, and therefore, regarding conformist bias in the Boyd & Richerson sense.

One such example is the question of whether positive frequency-dependent social learning arises because of normative or informative reasons. In Asch’s studies, following the majority was a response to peer pressure, but it does not have to be the case. Early on, Deutsch & Gerard (1955) remarked that social psychology had focused mainly on a single side of ‘conformity’ (here again understood as positive frequency-dependent social learning), namely, the normative side. In what they called normative social influence (later also referred to as *social* conformity, e.g., Coleman, 2004), the commonest behaviour defines a social norm that can be enforced, for instance by rewarding compliers and punishing non-compliers. In this case, conforming is simply avoiding punishment. The individual adoption of majority behaviour could occur through ordinary cognitive mechanisms for avoiding social and environmental risks, but also through the evolution of specific preferences that might have proved adaptive over long time scales even if avoiding punishment was not a conscious objective of individuals.

But Deutsch & Gerard described another driver of majority-following: informational social influence (sometimes also called *instrumental* conformity, cf. Burdett *et al.*, 2016). In this case, the behaviour of the majority does not define a norm, but instead it reveals useful information about the environment. Take the example of durian, a tropical fruit with a distinctly unpleasant smell which is widely popular in South-east Asia. The naïve tourist might be willing to try it in spite of the stench, not for fear of social sanctions if he or she does not, but rather because he or she can *infer* from observing the majority behaviour that the fruit is actually palatable.

Economists summarized the mechanisms and limitations of informational channel in a famous decision problem. Suppose that, on a night out and looking for a good dinner, you stumble upon two adjacent restaurants. One is crowded, the other almost empty. Which restaurant will you choose? First, you should realize that the behaviour of others probably conveys information about quality. The safest choice is therefore to follow the ‘wisdom of the crowd’ and go for the crowded restaurant (i.e., conform). However, sometimes the crowd is wrong, as Banerjee (1992) and Bikhchandani, Hirshleifer & Welch (1992) pointed out. Indeed, in this problem, the first few customers are pivotal in determining group behaviour: if they choose the lower-quality restaurant, all subsequent customers will copy their mistake. Such *informational cascades* were later observed in laboratory experiments with human subjects (Anderson & Holt, 1997). What these studies emphasized is the fragility of mass behaviour when it is driven by conformity, in the sense that it is susceptible to shifts when accurate information is publicly released. In our example, it means that if customers had had access to the restaurants’ ratings on Yelp or Tripadvisor, then they could have ignored the mistake of the first few customers and chosen the best restaurant instead despite its emptiness.

Economists also studied the normative channel. For instance, a shared concern for social status could lead most people to conform to a group norm, despite varying personal predispositions to follow that norm (Bernheim, 1994). Only individuals with a strong predisposition against norm behaviour will not conform, thus automatically flagging them as dissidents to the rest of the society. The social status of these nonconformists will be downgraded accordingly, with material consequences such as withholding of cooperation or direct punishment.

This informational vs. normative dichotomy, together with the above studies by economists, provides a convenient analytical structure for evolutionary biologists. They suggest that any tendency towards positive frequency-dependent social learning should be rooted in one of these two channels, i.e., that it should have normative or informational benefits. On the other hand, this analysis also suggests that positive frequency-dependent social learning is not always the right answer to an environmental challenge, as we will see more in detail below. Finally, as a particular case of positive frequency-dependent social learning, conformist transmission in the Boyd & Richerson sense should also obey these insights.

# III. CONFORMITY EVOLVES: A BENEFICIAL BIAS?

A few decades after Asch’s experiments, biologists incorporated conformity within the study of cultural evolution (Claidière & Whiten, 2012; Haun, van Leeuwen & Edelson, 2013; van Leeuwen & Haun 2013; Whiten, 2019, 2021). Integrating socially transmitted information into a population genetics framework raised the question of how individuals use social information to maximize fitness (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985). This predicts that such socially aware individuals would be equipped with a wide range of social transmission biases that dictate whom they copy and when (Feldman, Aoki & Kumm, 1996; Henrich & Boyd, 1998; Henrich & McElreath, 2003; Laland, 2004; Enquist, Eriksson & Ghirlanda, 2007; Wakano & Aoki, 2007; Kendal *et al.*, 2009). For instance, individuals could preferentially copy prestigious models (prestige bias), or models that look like themselves (similarity bias), or even – our focus here – models that display the majority behaviour (conformist bias, or *conformity* for short). A rigorous definition of conformity was established early on by Boyd & Richerson (1985): an individual is *conformist* if it is more likely to adopt the majority behaviour than if it copied a demonstrator picked at random (Morgan & Laland, 2012; Muthukrishna, Morgan & Henrich, 2016; see Fig. 1). Given the right conditions, this ‘over-copy-the-majority’ rule could be highly profitable.

Subsequent evolutionary models examined conditions favouring different learning biases. Conformity’s ‘sweet spot’ turned out to be a spatially variable environment with migration, since conforming helps migrants to quickly adopt the locally adaptive behaviour (Henrich & Boyd, 1998; Boyd & Richerson, 1985; reviewed in Aoki & Feldman, 2014). More generally, conformists perform better when environmental change is slow, social learning is easy (relative to individual learning), transmitted traits have high adaptive value, and fitness payoffs vary a lot with space (Nakahashi, 2007; Kendal *et al.*, 2009).

Conformity adds robustness in the transmission process overall (Dindo, Whiten & de Waal, 2009; Danchin *et al.*, 2018; Lachlan, Ratmann & Nowicki, 2018). A conformist learner is unlikely to pick up a one-off behavioural mistake, since its decision is based on many demonstrators. Yet this redundancy also dampens innovation (Sterelny, 2006), and in rapidly changing environments, it may cause a carryover of old behaviours that are no longer adaptive if the individuals are not flexible enough to adapt at the same speed as the environment changes (Aplin *et al.,* 2017). In the context of cultural evolution, this can in turn slow down the response to environmental change and thus promote the maintenance of outdated maladaptive behaviours (Whitehead & Richerson, 2009).

Crucially, conformity generates a stable combination of within-group homogeneity and among-group heterogeneity. Indeed, conformity fixes a given group on a single socially learnt tradition that remains stable over generations, making the tradition resistant to erosion and robust to invasion of alternative variants. Importantly, different groups can fix on different traits depending on which trait is locally optimal, cultural drift or some specific initial conditions for instance.

Conformity does not necessarily foster the adoption of optimal traits as it can stabilize any trait given the right conditions (Laland, 1994). For example, conformity can foster cooperation if interactions and learning are spatially constrained in the population, thus giving rise to ‘local clusters’ of co-operators (Peña *et al.*, 2009; Mengel, 2009; Molleman, Pen & Weissing, 2013). Instead, in large homogeneous populations, cooperation is diluted, and conformity can block its evolution (Lehmann & Feldman, 2008; Molleman, Quiñones & Weissing, 2013). Similarly, conformity can coevolve with other cultural or genetic traits such as altruism (Lehmann & Feldman, 2008) or the ability to copy (Wakano & Aoki, 2007).

These models have provided extensive insights into how conformity works, but some questions remain unexplored, as we discuss below.

## (1) Looking for normative conformity in non-human animals

All the evolutionary models mentioned above relate to *informational* benefits of conformity. They depict cases where the majority behaviour is a local fitness-maximizing social cue. Hence, predicting the evolutionary success or failure of conformity rests on the statistical concept of *Bayesian inference,* as made explicit by Perreault, Moya & Boyd (2012). All models thus follow more or less the same reasoning, at least implicitly. They (i) take a naïve individual seeking the fitness-maximizing alternative amongst several behaviours; (ii) assume that the best behaviour is selected for so that it increases in frequency; (iii) hence, conclude that the most-displayed behaviour should be the best, provided that the demonstrator population had enough time to undergo selection. Although this reasoning holds under many circumstances, it may fail when the environment is too unstable for the demonstrator population to have reached the best strategy.

In the normative case, benefits instead occur when the population itself rewards a given behaviour (the norm), or punishes non-compliers. Administering these rewards or punishments is often costly, which impedes the evolution of such social machinery. However, conformity can overcome this evolutionary obstacle so that hardwired conformity allows costly social norms to evolve, implying that conformity might be responsible for the emergence of a reward-and-punishment culture (Henrich & Boyd, 2001). Once established, costly social norms can even coevolve with conformity (Gúzman, Rodrίguez-Sickert & Rowthorn, 2007) although such associations are harder to obtain than previously thought (Van Cleve, 2016). Since conformity also accounts for the stable combination of intergroup heterogeneity and intragroup homogeneity, it can in turn trigger cultural group selection (Boyd & Richerson, 1985).

Until now, informational benefits have been the dominant explanation for conformist behaviour in evolutionary biology (for an extended discussion see Claidière & Whiten, 2012). Nonetheless, in a non-conformity context rewards or punishments for complying (or not) with group specific rules or norms have been documented in animals (Singh & Boomsma, 2015; reviewed by Raihani, Thornton & Bshary, 2012) particularly in insects and non-human societies where it seems to maintain intense levels of cooperation, suggesting the existence of normative benefits in non-human animals. We thus suggest that the normative channel deserves more attention.

## (2) Viability of conformity in strategic settings

Is it always beneficial to copy the majority? As a preliminary answer to this question, consider how you, as a conformist individual, might fare in the following three scenarios.

1. Choosing between two plentiful food sources, each potentially healthy or poisonous.

2. Choosing between two identical but limited-supply food sources.

3. Choosing between two paths to avoid a predator that preys preferentially on smaller groups.

Scenario 1 is a straightforward win for informationally driven conformity: if a majority of people feed from a given food source, it probably means that it is healthy, so conforming is a good bet. That changes, however, in scenario 2: since the food sources are in limited supply, the more individuals feed from one, the less food remains for you there. Here, conforming will not work well: the situation calls for *not* copying the majority, and you would be better off by taking the less popular option. In scenario 3, conformity makes a comeback: the more individuals take a given path, the less likely you are to be attacked by also taking that path (Cresswell & Quinn, 2011). To improve your chances of survival you should learn which is the safe way according to the number of individuals using it, i.e., copy the majority.

The crucial difference between these scenarios is how the behaviour of others affects your fitness. In scenarios 2 and 3 the viability of each option depends on what others do – neither option is intrinsically better independently of the actions of others. Economists call such interactions *strategic*. In scenario 2, those you copy affect your fitness *negatively*. Such behaviours are called *strategic substitutes*, which means that the attractiveness of an option decreases as more individuals choose it (negative frequency dependence).In scenario 3, those you copy affect your fitness *positively* – such behaviours are called *strategic complements*, which means that the attractiveness of an option increases as more individuals choose it (positive frequency dependence) (Bulow, Geanakoplos, & Klemperer, 1985). Scenario 1 is non-strategic as there *is* an intrinsically better option (the healthy one) and the behaviour of others affects your fitness only insofar as it provides social information on what that better option is.

These scenarios sketch a qualitative result: conformity seems to thrive only when behaviours are strategic complements, or non-strategic. While a rigorous theoretical exploration may be needed to confirm this simple intuition, it suggests that strategic complements or substitutes may provide a useful lens to understand why conformity evolves for some traits but not others. Further research is needed, both on theoretical and empirical fronts, to investigate this potential link between conformity and strategic settings.

## (3) Information acquisition, the value of observations, and memory

As a matter of fact, the classical formalisms used to model information acquisition are idealized largely. Models commonly assume a simple group structure where individuals observe *simultaneously everyone else* in their group, and then infer the majority behaviour from this far-reaching, sweeping look. Especially when more than three role models are observed the evolutionary dynamics can be more complex than previously thought (Krebs Denton *et al.*, 2020). More realistically, observations in fact are gathered *sequentially* from a *subset* of the whole population (Morgan, Acerbi & van Leeuwen, 2019), as in a recent study on chimpanzees (*Pan troglodytes*; Watson *et al*., 2018). Organisms must deduce the majority behaviour from such imperfect samples, probably by using individual learning and memory, which none of the models of conformity we know has implemented. Different environments could promote different ways to deal with information. In unstable environments for instance, older observations may be discounted in favour of recent ones, since reliance on past observations could cause deleterious behavioural inertia.

Similar arguments hold for how to integrate space, prestige or other characteristics into the evaluation of observation. Should an immigrant completely ignore information from its home environment in favour of local practices? Should it give more weight to demonstrators similar to itself? Is a prestigious demonstrator worth two, ten, or a thousand ordinary ones? Mesoudi (2018) addressed similar questions by modelling immigrant conformist acculturation. Basically, this comes down to studying the interaction between conformity and other biases, such as prestige, success, locality, ethnicity, age, sex, etc. The core problem is to determine the value of adding a single demonstrator into the decision process, based on that demonstrator’s personal characteristics relative to the observer. This is both a theoretical and an empirical question that needs to be explored.

Finally, while most current studies concern binary choices, natural situations usually involve many more options. Expanding the binary approaches would raise empirical challenges (what would occur when the majority is still an absolute minority, as in a 40–30–30 split?) and theoretical ones. A first unanswered problem is to devise a suitable learning rule (a S-shaped probability, symmetric in all behaviours) when there are more than two behaviours to choose from, or even when traits are continuous. These issues remain under-explored for the moment, with few exceptions (e.g., Nakahashi, Wakano & Henrich, 2012; Mesoudi, 2018). In the next paragraph we outline a possible step in this direction.

## (4) Conformity with more than two choices: a functional form and a statistical test

The canonical mathematical model for conformist transmission is the sigmoid curve (Fig. 1 red lines) proposed by Boyd & Richerson (1985) in their initial work on conformist transmission and cultural evolution (Fig. 1a). Their model considers the case with two traits. If we call *q* the proportion of trait A in the population, and 1*-q* the proportion of trait B, then Boyd & Richerson defined the probability *p* that an individual will adopt trait A as

*p*(*q*) = *q* + β*q*(1-*q*)(2*q*-1)

where β is a parameter between 0 and 1. This model conveniently encapsulates the essential feature of the conformist bias, i.e., that an individual is disproportionately likely to adopt the majority variant. However, as can been seen on Fig. 1a, it covers only a small fraction of all possible S-shaped curves. In particular, it cannot account for very steep slopes around *p* = 0.5. On the other hand, empirical work has shown that individuals can be surprisingly efficient in detecting majorities around 50%, leading to a sharp behavioural response to demonstrator frequencies that can look more like a step function than a mild sigmoid curve (Aplin *et al*., 2017; Danchin *et al*., 2018). Does a model exist which can accommodate these very steep slopes, and (ideally) that could also be generalizable to the case with any number of traits?

One such model could be McFadden (1973)’s discrete choice model, which is commonly used in economics to describe consumer choice. In this model, the probability of adopting trait A takes the logistic form

*p*(*q*) = *q*^β/(*q*^β + (1-*q*)^β)

where β is a parameter which can be any real number. This model can be micro-founded by considering that learners pick up the most common trait but may be subject to random deviations. As can be seen from Fig. 1b, this alternative model is very comprehensive for describing milder to stronger forms of conformity in Boyd & Richerson’s sense. Furthermore, it also accommodates other learning rules, which sometimes have been called ‘weak conformity’ and ‘anti-conformity’ (see Whiten, 2019). Specifically,

1. β > 1 corresponds to conformist transmission in Boyd & Richerson’s sense,
2. 0 < β < 1 corresponds to weak conformity,
3. β < 0 corresponds to anti-conformity.

These three cases also suggest a simple statistical test for conformity. Assuming that one has data on individual behavioural responses as a function of demonstrators’ behavioural frequencies *q*, testing for whether these behavioural data exhibit conformity is then straightforward: the data must fit the model for a value of β greater than 1. To test this, simply remark that

ln[*p*(*q*)/(1-*p*(*q*))] = β \* ln[*q*/(1-*q*)],

i.e., that there is a linear relationship between the log odds of the response probabilities and the log odds of the demonstrators’ frequencies, with the associated slope being β. The value of β can thus be obtained by performing a simple linear regression, since the log odds are immediately available from the data. Whether this coefficient is significantly above 1 should be evidence for conformist bias.

A convenient feature of this model is that it can be easily extended to any number of traits,

*p*\_*a*(*q*) = *q*\_*a*^β /(sum\_*i* *q*\_*i*^β).

A corresponding statistical test can then be derived from the following equality, valid for any two traits a and b:

ln[p\_a(q)/p\_b(q)] = β \* ln[q\_a/q\_b].

Lastly, both Boyd & Richerson’s mathematical model and the one we propose above fail to account for individual departures from unanimous majorities (i.e., few learners picking up trait B when 100% of demonstrators show trait A; see Fig. 1a). Yet, such occurrences were documented as early as Asch (1955) and have been corroborated in many animal studies of conformity (e.g., Battesti *et al.*, 2015; Pike & Laland, 2010; Aplin, Sheldon & McElreath, 2017; Danchin *et al.*, 2018). This phenomenon could for instance be evidence of major cognitive limitations, or of important heterogeneities within populations regarding learning rules. In any case, this feature seems ubiquitous and may lead to false negatives when using the statistical test suggested above. A simple extension of the model above can however address it. Consider that the learner chooses a trait at random with probability α, and chooses a trait using the conformist rule *p*(*q*) above with probability 1-α. In the case with two traits, the probability of adopting trait A becomes

*p’*(*q*) = α / 2 **+** (1-α) \* *q*^β/(*q*^β + (1-*q*)^β).

Once again, one can estimate this equation on behavioural data and check whether β>1 for evidence of conformist transmission in Boyd & Richerson’s sense.

# IV. ANIMAL CONFORMITY

## (1) Behavioural ecology

Boyd & Richerson’s conformist transmission model has recently attracted a lot of attention in behavioural ecology (e.g., Pike & Laland, 2010; Nelson & Poesel, 2014; Aplin *et al*., 2015a, 2017; Battesti *et al*., 2015; Danchin *et al*., 2018; Lachlan *et al*., 2018; Ayoub, Armstrong & Miller, 2019; Brown & Lachlan, 2002), the domain of evolutionary sciences that studies the evolution of behaviour (Davis & Krebs 1984; Danchin, Giraldeau & Cézilly 2008). However, although conformity in humans rapidly attracted attention, it remained largely overlooked in animals for a long time, with the first studies of animal conformity being published in the early 2000s, more than 50 years after Asch’s studies. Although animal conformity is now becoming a hot topic, the junction with the domain of human conformity remains to be made to allow the full study of the evolutionary origin of human conformity.

In the animal literature, conformity is often defined as 'behaving like, or copying, the majority' which is in many cases a simplification of Boyd & Richerson’s 'disproportionate likelihood of adopting the majority strategy' definition. That broader definition raises at least several important issues. First, that definition does not specify whether the majority concerns the larger number of individuals performing a behaviour or whether it concerns the behaviour that is most frequently displayed (van Leeuwen *et al.*, 2015). In fact, it is interesting to notice that this is not specified in Boyd & Richerson´s model either. From an evolutionary standpoint, the majority should concern the number of individuals performing a behaviour. Otherwise, there might be only a few individuals over-displaying a given behaviour, making it the most frequent, but not the one adopted by the majority of the population (van Leeuwen *et al.*, 2015; Acerbi *et al.*, 2016). However, in some cases it might be the highly skilled or successful individuals that perform one of the options at high frequency. Thus, conforming in relation to the frequency of the performed options may be as adaptive as conforming in relation to a majority of individuals (Aplin *et al*., 2015b). Similarly, models showed that the number of individuals and the frequency of the behaviour can lead both to the same sigmoidal conformity curve (Smaldino *et al.*, 2018). Second, this simplified definition of conformity is sometimes used only for cases where an individual performing behaviour A *changes* to behaviour B to follow the majority (e.g., Cialdini & Goldstein, 2004; Cherng *et al.*, 2014; Haun, Rekers & Tomasello, 2014). This restriction seems unnecessary as naïve individuals can also show conformist behaviour after observing others. Last but not least, it is important to focus on the fact that copying the majority without exaggerating cannot foster within-group stable traditions. This is illustrated in Fig. 1 where Boyd & Richerson's definition of conformity corresponds to the grey areas, while the common broader definition of conformity would also consider strategies in the blue areas as conformist, despite the fact that such strategies would invariably rapidly drive populations towards a stable equilibrium with no majority (i.e., at 0.5). Thus, the 'disproportionate likelihood of adopting the majority strategy´ is crucial to study and compare conformity both in animals and humans.

Although research on animal conformity is relatively recent, there is some evidence for conformity in several taxa from insects to great apes and in various contexts including foraging, song learning, problem solving tasks, tool use and mate choice (Tab. 1). Unfortunately, it appears that all these studies use very different kinds of definition of conformity ranging from a copy the majority rule, over Aschian conformity where a personal preference/behaviour is replaced by the majority preference/behaviour to Boyd & Richerson’s definition of conformist transmission. Thus, the field would benefit from clearer definition and consistent use of the terminology to allow for comparisons between species and studies. More generally, Tab. 1 does not include the well-studied phenomena of herding or shoaling and other processes of aggregation (as for instance coloniality in birds, e.g., Siegel-Causey & Kharitonov, 1990; Buckley, 1997; Danchin & Wagner, 1997; Danchin, Boulinier & Massot, 1998; Dukas & Edelstein-Keshet, 1998; Rolland, Danchin & de Fraipont, 1998; Doligez *et al.*, 1999; Barta & Giraldeau, 2001; Brown & Bomberger Brown, 2001; Serrano *et al.*, 2001; Boulinier *et al*., 2002; Doligez, Danchin & Clobert, 2002; Eberhard, 2002; Doligez *et al*., 2003; Parejo *et al*., 2007; Varela, Danchin & Wagner, 2007) that are not usually called conformity, despite the fact that such processes can be envisioned as forms of conformity in space as long as they involve social learning, which was clearly suggested by several authors by both observational and experimental data (Doligez, Danchin & Clobert, 2002; Doligez *et al*., 2003; Parejo *et al*., 2007).

Similarly, we did not include the vast literature about mate copying as there is a recent review on that topic (Varela, Matos & Schlupp, 2018). The reasoning using the Fisher runaway process, which we develop in the next section for the origin of social learning and conformity, also applies to mate copying, which is a special case of social learning in the context of mate choice in which females build their own preference on the observation of another female choosing between male phenotypes. After all, mate copying and conformity in mate choice bear many similarities in that they both concern social learning in a mate choice context. This raises the question of the links between these two processes. Mate copying can be performed in a conformist manner, i.e., copying what is preferred by the majority on one hand, and on the other hand conformity in mate choice can be the result of positive frequency-based mate copying. Unfortunately, very few studies of mate copying have tested whether it is performed also in a conformist fashion, forbidding us from studying the links between these two processes. In fact, most studies on mate copying use only a single demonstration for practical reasons, thus preventing us from talking about the majority. Mate copying can in fact be looked at as a specific case of conformity in which the sample size of demonstrators is only 1. As soon as there is a majority preference in a population, chance makes it more likely that this single observation represents the local majority. But the fainter the majority the higher the risk of opting for the locally non preferred male phenotype (this corresponds to the black random copying line in Fig. 1). By observing multiple matings, if possible, observer females can considerably increase the quality of their assessment of the local majority and thus can considerably increase their chance of building a preference for the majority male phenotype. Nonetheless, if future studies show that mate copying is commonly displayed in a conformist manner, it would suggest that these two processes are linked, and both mate copying and conformity in mate choice would associate in accelerating and maintaining the evolution of local traditions for preferring a specific male phenotype over many generations. Thus, future studies should systematically test for conformity in mate copying.

All these considerations suggest that there is probably more evidence for the existence of informational conformity in animals than usually thought. This vast breadth of taxonomies and contexts raises the question of the evolutionary origin of conformity. In itself, this breadth suggests convergent selection for conformity rather than a homologous capability (Laland, Atton & Webster, 2011). However, we are still lacking a general framework by which conformity may have emerged during the course of evolution.

## (2) Conformity in mate choice and the Fisher runaway process

Our review of the literature on animal conformity has revealed a quasi-absence of evidence for conformity in the context of mate choice (Tab. 1). The only example of conformity in mate choice is a study in fruit flies (*Drosophila melanogaster*) where females develop mating preferences for a certain male phenotype in a conformist manner (Danchin *et al*., 2018). In that study, as long as there was a majority of demonstrator females copulating with males of a given phenotype, observer females copied this choice and developed a similarly significant bias for males of that specific phenotype whatever the level of majority in the population. As a result, the response function of observer females followed a step function (as the blue curve of Fig. 1), with females learning equally well to prefer the most commonly chosen male colour whatever the level of majority, which in that study varied experimentally from 100% to only 60%. However, a certain number of individuals did not copy the majority for whatever reason (e.g., being anti-conformists or individual learners). A simple model also suggested that this strong conformity in mate choice might generate surprisingly long-lasting traditions of preferring one male phenotype at the local scale (Danchin *et al*., 2018).

The drosophila result on conformity calls for an evolutionary explanation. Interestingly, conformity in the context of mate choice is reminiscent of the well-known Fisher runaway process (Fisher, 1930). We now propose and provide a generic model for a possible two-step evolutionary scenario rooted in this process, which unfolds at two different spatial scales.

Let us first imagine an ancestral metapopulation with two heritable male phenotypes A and B. There is no initial female preference for one of these male phenotypes, but some heritable (genetic or non-genetic) variation in females' tendency to copy others. In a given subpopulation, chance may sometimes lead to more females mating with, for instance, A males. As soon as such a majority becomes detectable, copier females tend to mate more often with A males. As a result, they will tend to have A sons and daughters that tend to copy the choices of their elders, implying that they reject B males (left panel, Fig. 2). At the scale of the subpopulation, this reinforces both the proportion of A males and the tendency to socially learn to prefer A males. On the other hand, females of the initial subpopulation choosing B males (i.e., mostly non-copiers) would have B sons and mostly non-copier daughters that mate randomly with A and B males. So, at the beginning, while copier females tend to amplify the proportion of A males and the tendency to copy, non-copier females produce 50% of A and 50% of B sons, while producing non-copier daughters.

Thus, at the scale of the subpopulation, locally both the proportion of A males and of copier females slowly increase with a rate that accelerates with the proportions of copier females in a kind of snowball effect. As a result, non-copier females mating with B males will have B sons that will be more and more socially unsexy over the course of generations. On the other hand, copier females mating with A males are more and more favoured (left panel, Fig. 2). In summary, at the local scale, this process transitorily selects for A males, and for social learning in mate choice, as social learning becomes neutral after the local disappearance of the B male phenotype (see simulations in the left panel of Fig. 3). Note that even if the two male phenotypes initially did not differ in terms of fitness, the trait soon quits neutrality because of the social transmission of mating preferences in females. This is the runaway process.

Now, this logic unfolding within a single subpopulation should simply transitorily select for females preferring A males. However, at the scale of a metapopulation, which consists of subpopulations connected by dispersing individuals, in some subpopulations selection would favour females mating with A by chance (left panel, Fig. 2), and in others subpopulations females mating with B males (right panel, Fig. 2). In such a system, dispersal hampers the local evolution of a heritable preference for A, and favours conformity, as immigrants detecting the local preference and conforming to it have higher fitness (right panel Fig. 2, and Fig. 3). Hence, it is the spatial structure of the metapopulation with individuals dispersing among subpopulations that generates selection for the more integrated rule of 'mate with males of the *locally* preferred phenotype', i.e., for conformity.

Note that this process is superficially similar to a process by which conformity could arise for foraging preferences, but it is different at a deeper level as in the latter case conformity evolves due to natural and not sexual selection as proposed above. Suppose that in the first subpopulation fruit C is nutritious and fruit D is poisonous, while in the second subpopulation there is fruit E, resembling C, that is poisonous and fruit F, resembling D, that is nutritious. A preference for C and a preference for copying the majority would be equally adaptive in the first subpopulation, just as a preference for F and a preference for copying the majority would be equally adaptive in the second subpopulation. However, for dispersers between the two, a preference for copying the majority would continue to be adaptive, while a preference for C, translated to the second environment, might be fatal, as would a preference for F, translated to the first environment. So, conformity would be more adaptive on average than either direct nutritious preference.

Unlike the Fisher process, though, this process would not be self-reinforcing - conformity would not become more adaptive as it became more common in the population. In addition, its adaptive value would depend on the absence of consistency in the nutritious value of foraging preferences across environments. This may be true in some ecologies but lacks the general autocatalytic runaway character of the Fisher process, which is independent of other characteristics of the environment.

In view of the generality of the Fisher runaway process in sexually reproducing organisms, and in view of its autocatalytic properties, we can predict that conformity in mate choice might be far more common than usually understood. In particular, the abundant literature on mate copying (which can be viewed as hinting at conformity in sex) suggests that these capacities exist in all vertebrates and at least some insects. It is thus of prominent importance to design experiments that actually manipulate the level of majority in order to study the response function of conformity in mate choice in a vast range of species.

# V. FROM FISHER TO HUMAN CULTURE

Beyond the fact that the existence of conformity in numerous animal taxa generates a continuum from animals to humans, it is necessary to integrate some of the major consequences of the evolutionary scenario presented in the previous section in terms of its potential to foster cultural transmission in general and in humans in particular.

As said before, the first step in this evolutionary pathway unfolds locally and temporarily favours social learning (Step 1 of Fig. 4). Similarly, the second component results from individuals dispersing among subpopulations within the metapopulation, which stabilizes social learning and leads to the evolution of conformity (Step 2 of Fig. 4). Thus, in highly mobile species, conformist mate choice must have fostered the development of a kind of 'conformist module' for detecting the majority and following it in order to preferentially mate with the locally preferred male phenotype. These two first steps are detailed in the previous section and should foster the emergence of local traditions in mating preferences (Step 3 of Fig. 4).

However, the story does not end there. We have detailed above that there is some theoretical and empirical evidence that conformity is potent in fostering a cultural process (Fisher, 1930; Sterelny, 2006; Efferson *et al*., 2008; Laland *et al*., 2011; Danchin *et al*., 2018; Lachland *et al*., 2018). Like norms or punishment, conformity can play the role of a “repair mechanism” to maintain an existing preference/behaviour. Thus, once acquired and potent, the conformity module may have percolated to other contexts such as foraging, problem solving, tool use, etc. (Step 4 of Fig. 4). Alternatively, cognitive processes involved in copying foraging behaviour may have been subsequently co-opted for use in mate choice. Some mechanisms, however, do not seem easily co-opted from foraging to mate choice - for instance, the pheromone trails that yield conformity in ant foraging (Sumpter & Beekman, 2003). Another alternative is that conformity emerged independently in foraging and mate choice within lineages. Further studies are needed to rule out the different possibilities. Nonetheless, as in this scenario initial fitness benefits accrue from reproduction, it predicts that social learning should remain efficient during the whole reproductive period, which appears consistent with some animal and human studies.

The evolution of a conformity module that expanded to other contexts then may have fostered the emergence of local traditions in many domains of behaviour (Step 5 of Fig. 4). This pathway would thus imply that all the reported cultural processes in animals, whatever the domain involved, would find their origin in mate choice and sexual reproduction, because of the initial trigger of the Fisher runaway process.

The potential relevance of mate copying for the evolution of conformity is also valid for humans (Step 6 in Fig. 4). Our hypothesis suggests that all our cultural skills (including the most exquisite arts, religions and beliefs), may have originated in our ancestors as a consequence of the basic and unavoidable importance of finding the best mate, which as we explain here, must imply detecting what kind of mate is preferred in the population and conforming to it.

We investigate the verbal model described informally above using simulations. Consider a group of individuals, with the same number of males and females. There are two diallelic genes. The first one, with alleles *A* and *B*, is expressed in males only and is neutral for fitness. The second one, with alleles *C* and *c*, is expressed in females only: females *c* mate randomly, while females *C* use the logistic conformist learning rule described in section III.4. Each female has two offspring, one male and one female that inherit the traits from their parents.

The meta-population is composed of several such groups. In each new generation, a random fraction of the offspring migrates to another randomly chosen subpopulation on one of the spots left vacant by other migrants (males take male spots and females take female spots to prevent gender bias in groups). Initially, alleles *A* and *B* are randomly allocated in the meta-population in 50:50 proportions. Alleles *C* and *c* are also randomly allocated, with an initial proportion *q*0 of allele *C*.

The results of the simulations can be shown on Fig. 3 for a specific set of parameters. When the population is structured into subgroups, conformity can evolve, and leads to among-group diversity on the male phenotype. This can be compared to the case where the population is unstructured (same number of individuals but no subgroups and therefore no migration), where male diversity is quickly lost, and conformity becomes neutral.

# VI. CONCLUSION

The strength of our proposed pathway rooted in mate choice and runaway sexual selection is that it explains the evolution of social learning and conformity, as well as culture. One of the major challenges therefore for empirical studies of social learning is to find out whether the detection of majority behaviour in mate-copying preceded (in evolutionary time) the detection of majority behaviour in other contexts such as foraging and to what extent it evolved analogously or homologously. For that goal we will need to determine the shape of the response function of conformity in mate choice, and in other contexts with experiments manipulating the level of majority in a vast range of species. Altogether, this provides a rich agenda for future research. In the expectation of such information, the tentative model we propose and simulate here for the evolution of conformity, and all its cultural evolution consequences, casts surprising light on one of the major processes that has participated in making us humans; everything might have originated with sex.

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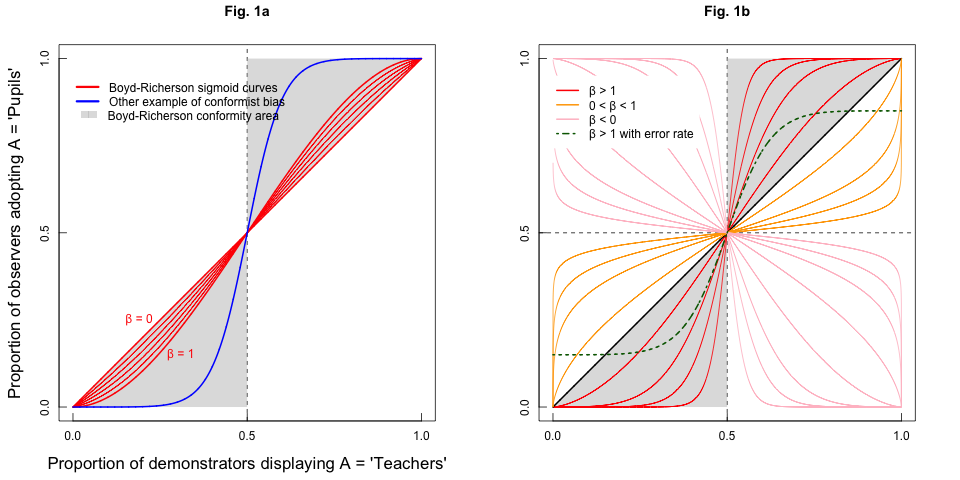
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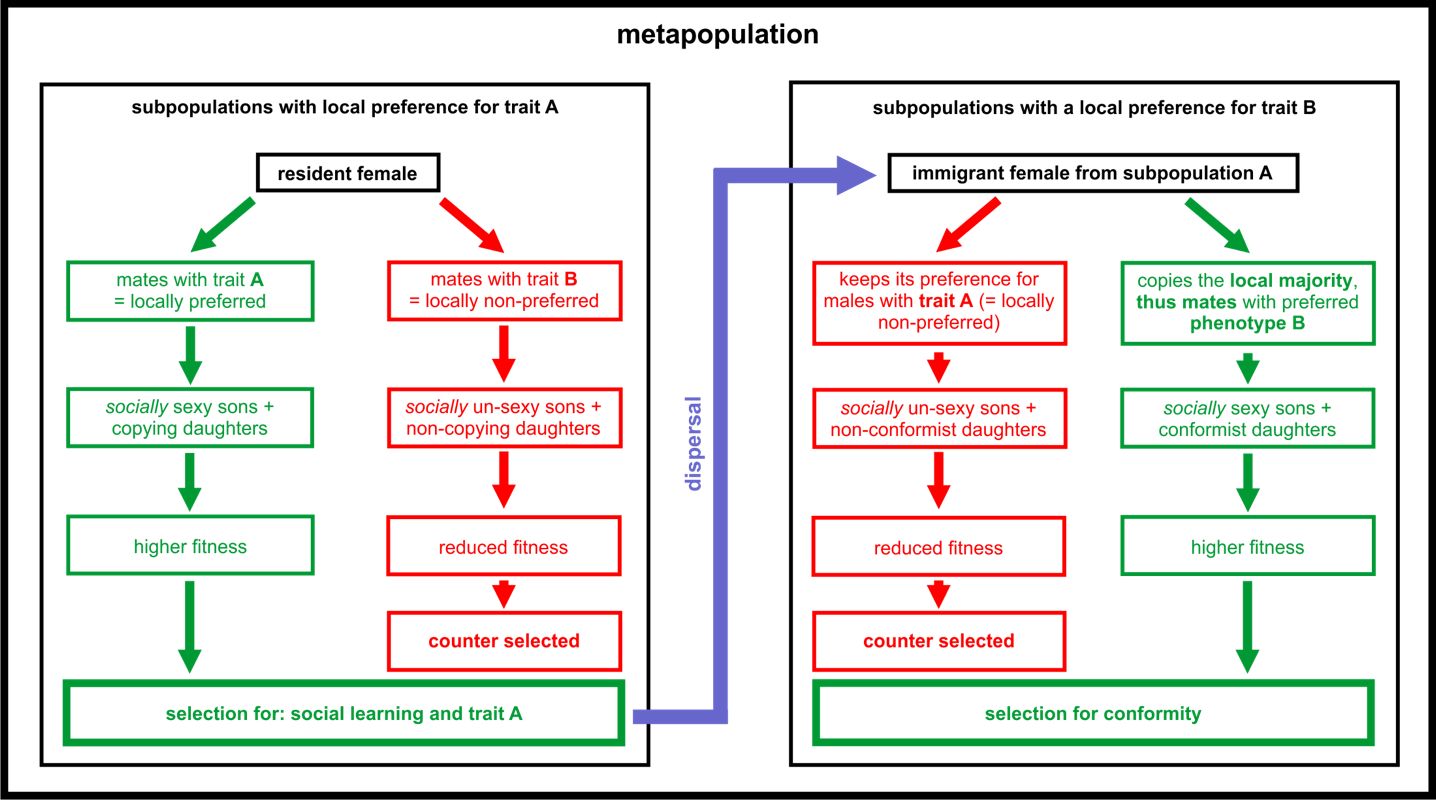
# Table and figures

**Table 1:** Reported examples of conformity in the animal kingdom. Here, we only reviewed instances when the authors explicitly referred to conformity (see text for comments on this choice).

|  |  |  |  |
| --- | --- | --- | --- |
| **Species** | **Context** | **Working definition used** | **References** |
| ants (*Paratrechina longicornis*) | cooperation | “conformist group members align their actions with those of their neighbours” | Gelblum *et al.*, 2015 |
| fruit flies (*Drosophila melanogaster*) | oviposition site, mate choice | “the tendency to disproportionately adopt the most commonly encountered social information”  “an exaggerated tendency to copy the majority” | Battesti *et al*., 2015;  Danchin *et al*., 2018 |
| solitary crabs (*Carcinus maenas*) | personality | “animals compromise their own behaviour to the level of a certain behaviour displayed by another individual or a group” | Fürstbauer & Fry 2018 |
| guppy (*Poecilia reticulata*) | shoaling, foraging | "many animals are disproportionately likely to adopt via social learning the behaviour of the majority”  “strong compulsion for individuals within social groups to remain in close contact and look and behave similarly”  “positive frequency-dependent social learning” | Brown & Laland, 2002;  Brown & Irving, 2014;  Day *et al.*, 2001 |
| mosquitofish (*Gambusia holbrooki*) | shoaling | No clear definition *(“behave like others”)* | Herbert-Read *et al.*, 2013 |
| rummy-nose tetra (*Hemigrammus*  *rhodostomus*) | shoaling | “tendency to follow the majority of their neighbours nonlinearly“ | Lecheval *et al.*, 2018 |
| nine-spined sticklebacks (*Pungitius pungitius*) | foraging | “positive frequency dependent social learning where the probability of acquiring a trait increases disproportionately with the proportion of other individuals performing it” | Pike & Laland, 2010 |
| threespined sticklebacks (*Gasterosteous aculeatus*) | foraging | No clear definition *(“behave like others”)*  No clear definition *(“behave like others”)* | Webster & Hart, 2006;  McDonald *et al*., 2016 |
| zebrafish (*Danio rerio*) | foraging | “copy the majority strategy”  “individuals will appear to disproportionately copy the most common behavioural choice demonstrated by their group“ | Zala, Määttänen & Penn, 2012;  Ayoub, Armstrong & Miller, 2019 |
| Eurasian perch (*Perca fluviatilis*) | personality | “behaving uniformly”  No clear definition *(“behave like others”)* | Hellström *et al.,* 2011;  Magnhagen, 2012 |
| great tits (*Parus major*) | foraging, puzzle box | “individuals disproportionately adopting the most frequent local variant when first acquiring an innovation, and continuing to favour social information over personal information”  “disproportionate tendency to copy the most common behavioural variant” | Aplin *et al*., 2015;  Aplin *et al.*, 2017 |
| white-crowned sparrows (*Zonotrichia leucophrys*) | song | “when a young pupil models its song(s) on those of one or more tutors”  “disproportionate tendency to copy the most common behavioural variant” | Nelson & Poesel, 2009;  Nelson & Poesel, 2014 |
| swamp sparrows (*Melospiza georgiana*) | song | “disproportionate tendency to copy the majority” | Lachlan *et al*., 2018 |
| Gouldian finches (*Erythrura gouldiae*) | personality | “individuals will tend to synchronize their behaviour in time and space, altering their behaviour in line with their groupmates, and potentially suffering consensus costs” | King, Williams & Mettke-Hofmann, 2015 |
| Norway rats (*Rattus norvegicus*) | foraging | “changing one’s behaviour to match that of others” | Jolles, de Visser & van den Bos, 2011 |
| bottlenose dolphins (*Tursiops aduncus*) | foraging, song | “adopt the most frequent behaviour” | Cantor & Whitehead, 2013 |
| humpback whales (*Megaptera novaeangliae*) | foraging, song | “adopt the most frequent behaviour” | Cantor & Whitehead, 2013 |
| sperm whales (*Physeter macrocephalus*) | song | “learn preferentially the most common codas” | Cantor *et al*., 2015 |
| marmosets (*Callithrix jacchus*) | personality, puzzle box | no clear definition *(“behave like others”)* | Koski & Burkart, 2015 |
| redfronted lemurs (*Eulemur rufifrons*) | foraging | “adoption of the group’s norm, despite being in principle able to behave differently, or overriding of individually learned by socially acquired information” | Schnoell & Fichtel, 2012 |
| capuchin monkeys (*Cebus apella*) | foraging | “conform to the foraging preferences of their closest social partners, despite having the knowledge of alternative techniques”  no clear definition *(“behave like others”)*  no clear definition | Dindo *et al.*, 2009;  Crast *et al*., 2010;  Franz & Matthews, 2010 |
| white-faced capuchin monkeys (*Cebus capucinus*) | foraging | “the tendency for individuals to preferentially exhibit behavioural alternatives that they witness most frequently in their peers, or to exhibit the behaviours that are performed by peers who are considered most prestigious or successful, or those peers with whom they have the highest quality social relationships” | Perry, 2009 |
| vervet monkeys (*Chlorocebus pygerythrus*) | migration, foraging | “conformity to local behavioural norms” *(= “behave like others”)* | van de Waal, Borgeaud & Whiten, 2013 |
| Japanese macaques (*Macaca fuscata*) | tool use | “immature individuals should adopt the same type of stone-directed activities as most of the older group members” | Leca, Gunst & Huffman, 2010 |
| chimpanzees (*Pan troglodytes*) | foraging, puzzle box, tool use | “a powerful tendency to discount personal experience in favour of adopting perceived community norms”  no clear definition  “follow-the-majority (= the number of animals in a group performing a specific behaviour increases, so does the likelihood of a naïve individual adopting that same behaviour, thus driving the preservation)”  “the increased likelihood for learners to end up the behaviour demonstrated by most individuals”  “personal knowledge was dropped in order to adopt the behaviour of the group“  “previous knowledge is discarded under the influence of the majority of group members demonstrating an alternative tool selection preference”  “foregoing a pre-existing behaviour in favour of adopting one demonstrated by a majority of conspecifics” | Whiten, Horner & de Waal, 2005;  Whiten *et al*., 2007;  Hopper *et al*., 2011;  Haun, Rekers & Tomasello, 2012;  Luncz & Boesch, 2014;  Luncz *et al*., 2014  Watson *et al.*, 2018 |



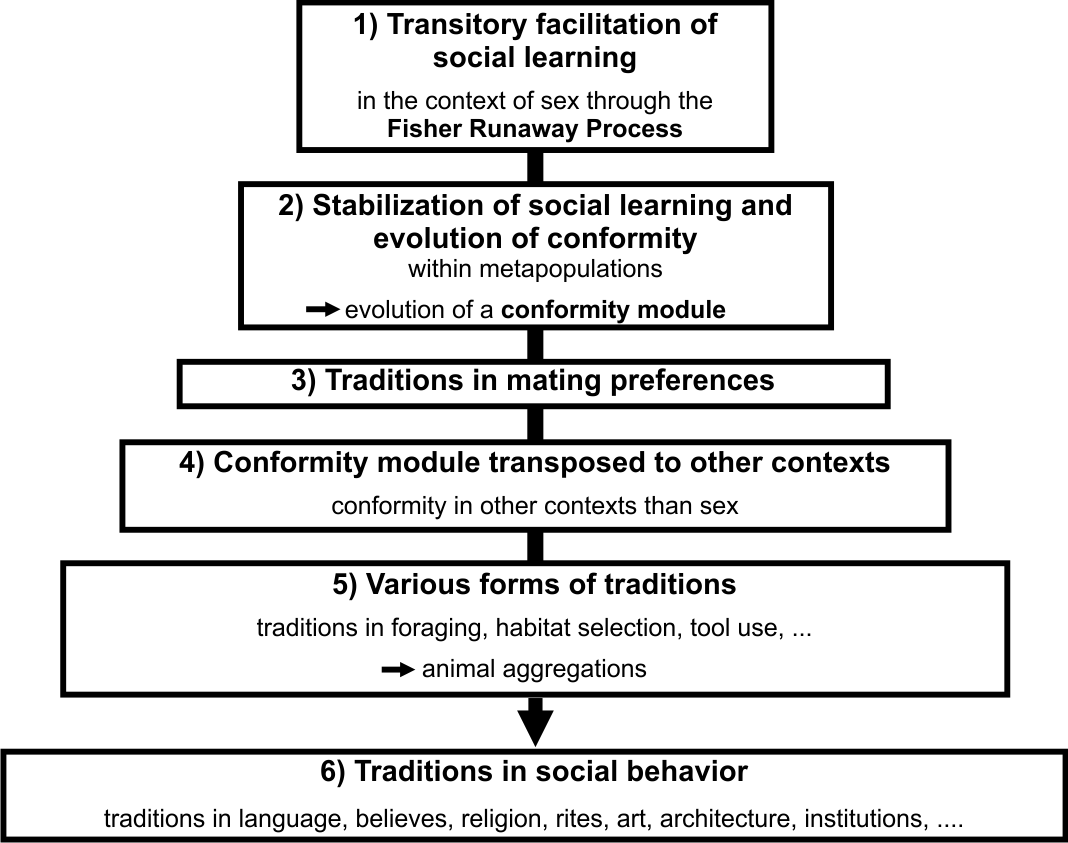
**Figure 1: An alternative functional form for conformity.** Both graphs depict the relationship between the proportion of demonstrators adopting one option (X-axis) and the probability that an observer subsequently adopts that option (Y-axis; in a case with two options). On the left (Fig. 1a) we show Boyd & Richerson’s definition of conformist bias. The grey areas correspond to conformity: observers are *disproportionately likely* to adopt the majority behaviour, i.e., more than under random matching (corresponding to β = 0). The red lines correspond to Boyd & Richerson’s mathematical definition of conformist bias: they only cover a small part of the area designated for conformity. The blue line corresponds to a conformist learning rule observed in real organisms (here that of Danchin et al. 2018 in the fruit fly). In effect, perfect conformity when getting close to 100% adopting the majority behaviour is highly unlikely in actual organisms. On the right (Fig. 1b) we show learning rules associated with the logistic expression from section III.4. This expression is flexible enough to cover Boyd & Richerson’s conformist bias or ‘hyper-conformity’ (red lines), as well as ‘weak conformity’ (orange lines) and ‘anti-conformity’ (pink lines). Using an error rate (green dashed line) it can also approximate empirical patterns of behavior whereby individuals depart from unanimous majority behavior.



**Figure 2: Social learning and conformity in mate choice are produced by the Fisher runaway process within metapopulations.** As females are usually the choosy sex, we illustrate that option. In some subpopulations, the majority of females mate with males of trait A while in others they prefer males of trait B. In red costly options (mating with the locally non-preferred male phenotype) and in green beneficial options (mating with the locally preferred male phenotype). Within subpopulations this selects for one male phenotype and social learning (left panel), but at the scale of a metapopulation dispersal leads to the selection for 'copy the majority', that is for conformity (right panel).

**Ein Bild, das Screenshot, Fenster enthält.

Automatisch generierte BeschreibungFigure 3: Conformity evolves in spatially structured metapopulations.** In a simple simulation model, we found that dispersal among subpopulations within a metapopulation can favour the evolution of social learning and conformity, which are well-known to be essential traits for the evolution of long-lasting local traditions, the main marker of a cultural process. Graphs obtained in simulations of the evolution of conformity in a population of non-copiers. Males express either trait A or B. Females are conformist or pick a male randomly. Lower graphs show conformity dynamics. Upper graphs show male trait dynamics. Left-hand graphs depict the dynamics within unstructured populations. Male diversity is quickly lost, and conformity remains neutral. Right-hand graphs depict the dynamics within structured metapopulations. Male diversity is maintained both among and very often within subpopulations, and conformity can evolve.

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**Figure 4: A tentative evolutionary pathway towards animal and human culture**. From the Fisher runaway process in the context of mate choice to social learning, conformity, traditions in sexual preferences, various forms of traditions including aggregated behaviour, and human culture.