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

Sabine Nöbel1,2\*, Antoine Jacquet1,3\*, Guillaume Isabel4, Arnaud Pocheville2, Paul Seabright1,3 & Etienne Danchin2

1 Institute for Advanced Study in Toulouse (IAST), Université Toulouse 1 Capitole, Toulouse, France.

2 Laboratoire Évolution and Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, IRD, 118 route de Narbonne, F-31062 Toulouse cedex 9, France.

3 Toulouse School of Economics (TSE), Université Toulouse 1 Capitole, Toulouse, France.

4 Centre de Recherches sur la Cognition Animale, Centre de Biologie Intégrative, Université de Toulouse, CNRS, UPS, 118 route de Narbonne, F-31062 Toulouse cedex 9, France.

\* equal contribution

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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 the possibility to study the roots of human culture for decades. 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. The study of conformity started with Solomon Asch's famous experiment in humans in 1955. Contrastingly, evolutionary biologists really started to be interested in conformity at 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 will have sons, grandsons, etc. of the non-preferred phenotype, hence diminishing their fitness cumulatively 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 mate choice within a metapopulation. In a generic model, we show that dispersal among subpopulations within a metapopulation can maintain independent Fisher runaway processes within subpopulations, and favouring the evolution of social learning and conformity, which are essential traits 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 humans; 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 the best mate. Based on our review, we further highlight several research avenues to better define the spectrum of conformity, and to account for its complexity. 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.

Table of Content

[ABSTRACT 2](#_Toc68073412)

[I. INTRODUCTION 3](#_Toc68073413)

[I. ASCH´S EXPERIMENT AND CONFORMITY BEYOND 4](#_Toc68073414)

[II. CONFORMITY EVOLVES: A BENEFICIAL BIAS? 6](#_Toc68073415)

[(1) Looking for normative conformity in non-human animals 7](#_Toc68073416)

[(2) Viability of conformity in strategic settings 8](#_Toc68073417)

[(3) Information acquisition, the value of observations, and memory 9](#_Toc68073418)

[(4) Identifying conformity in animals: Rethinking the mathematical definition 9](#_Toc68073419)

[III. ANIMAL CONFORMITY 10](#_Toc68073420)

[(1) Behavioural ecology 10](#_Toc68073421)

[IV. CONFORMITY INN MATE CHOICE AND THE FISHER RUNAWAY PROCESS 12](#_Toc68073422)

[V. FROM FISHER TO HUMAN CULTURE 14](#_Toc68073423)

[VI. CONCLUSION 15](#_Toc68073424)

[VII. ACKNOWLEDGEMENTS 15](#_Toc68073425)

[VIII. REFERENCES 16](#_Toc68073426)

# INTRODUCTION

Cultural processes have played and still play major roles in the evolution of humanity. A central process of cultural evolution is social learning through which information and adaptive responses can be transmitted and spread within and among populations (Laland, 2004; Rendell et al., 2011; Aplin et al., 2015). Social learning is ‘learning that is influenced by observation of, or interaction with, another animal or its products’ (Heyes, 1994). This definition includes a variety of processes where social factors influence the probability of acquiring public information and shape behavioural traits (Danchin et al., 2004).

A major characteristic of social learning for the establishment of cultural traditions and social norms is conformity (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Danchin et al., 2018). Conformity is defined as the *disproportionately likely* adoption of the most common variant within the local population (Boyd & Richerson, 1985). As such, conformity is a property of a group of individuals that can fix a single socially learned tradition that remains stable within a group over generations. 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 among-group heterogeneity.

Because of its central role for the emergence and maintenance of animal and human culture, conformity has long been a major topic of research in human sciences, and more recently and independently in evolutionary sciences (e.g., Banerjee, 1992; Bernheim, 1994; Whiten et al., 2005; Aplin et al., 2015; van Leeuwen et al., 2015; Danchin et al., 2018) so that we are still lacking a synthesis between these two scientific domains. 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.

1. ASCH´S EXPERIMENT AND CONFORMITY BEYOND

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. For his experiment, Asch invited college students to participate in a very simple 'visual judgment' task. In this task, he presented to groups of 7 to 9 students a drawing of three straight lines, alongside another reference line. Then, one by one, students had to announce in front of the group which of these three lines had the same length as the reference. Easy? It would have been, if not for a twist: before the experiment, all but one student were secretly instructed to give the same incorrect answer. An awkward half-hour ensued for the unaware student, as all other participants seemed to agree against what he saw. Very often, the unaware student ended up ignoring his own perceptual judgment, and instead aligned on the majority opinion. Asch (1955) ascribed this behaviour to social pressure and called this innate tendency to self-align on group opinion 'conformity.'

Asch’s momentous findings opened up the field of social psychology. They were replicated many times across different age classes and cultures, while varying group size, motivation, task difficulty or relevance (Baron et al., 1996; Bond, 1996; Bond & Smith, 2005; Griskevicius et al., 2006). Later, Latané’s (1981) work on ‘social impact theory’ provided a 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 status (such as prestige), or its proximity in time and space to the target individual (see also (Latané & Wolf, 1981)). Social psychology suggested a proximate reason for conforming, namely that people dislike going against the majority.

However, conformity is not only a response to peer pressure. Early on, Deutsch & Gerard (1955) underlined that social psychology focused mainly on a single side of conformity, namely, the normative side. In normative conformity (sometimes also called *social* conformity, e.g., Coleman, 2004), majority 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. This could occur through ordinary cognitive mechanisms for avoiding social and environmental risks, or through the evolution of preferences for adopting the behaviour of the majority, preferences that might have proved adaptive over long time scales even if avoiding punishment was not a conscious objective of individuals.

The other side of conformity is *informational* (sometimes also called *instrumental*, cf. Burdett et al., 2016). In informational conformity, the behaviour of the majority does not define a norm but reveals useful information about the environment. For example, most people eat and enjoy durian, a tropical fruit with a distinctly unpleasant smell. Of course, there is no risk of social sanctions if someone does not eat them, but it can be *inferred* from the majority behaviour that the fruit is palatable.

Economists summarized the mechanisms and limitations of informational conformity 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 et al. (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 normative conformity. 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 conformity dichotomy, together with the above analytical studies of economists, provides a convenient analytical structure for evolutionary biologists. Every conformist bias must reveal one of these two channels (informational or normative) depending on the specific benefits of conformity, a central question because conformity is not always the right answer to an environmental challenge, as we will see below.

1. CONFORMITY EVOLVES: A BENEFICIAL BIAS?

A few decades after Asch’s experiments, biologists incorporated conformity within the study of cultural evolution. Integrating socially transmitted information into a population genetics framework raised the question of how individuals use social information to maximize their 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 et al., 1996; Henrich & Boyd, 1998; Henrich & McElreath, 2003; Laland, 2004; Enquist et al., 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 et al., 2016; see Fig. 1). Given the right conditions, this ‘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 mild, social learning is easy, 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 et al., 2009; Danchin et al., 2018; Lachlan et al., 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. In the context of cultural evolution, this can in turn slow down the response to environmental change and thus promote the spread of outdated maladaptive behaviours (Whitehead & Richerson, 2009).

Crucially, conformity generates a stable combination of within-group homogeneity and between-group heterogeneity, which cannot be achieved through random copying alone unless there is enough genetic drift and migration. Indeed, with conformity a given group will fix on a single socially learnt tradition that remains stable over generations, is 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 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 et al., 2013a). Instead, in large homogeneous populations cooperation is diluted and conformity can block its evolution (Lehmann & Feldman, 2008; Molleman et al., 2013b). Similarly, conformity can coevolve together 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* conformity. They depict cases wherein the majority behaviour is a 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 et al. (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 normative conformity benefits 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 et al., 2007). 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 conformity has been the dominant explanation for conformist behaviour in evolutionary biology. Nonetheless, rewards or punishments for complying (or not) with social norms have been documented in animals (Singh & Boomsma, 2015; reviewed by Raihani et al., 2012) particularly in insects and non-human societies where it seems to maintain intense levels of cooperation, suggesting the existence of normative conformity in non-human animals. In a data set of 109 species of ants, bees and wasps where workers police each other to prevent individual workers from producing males, genetic relatedness appeared to significantly correlate with policing, but a great deal of the among species variation in policing remained unrelated to within colony relatedness (Wenseleers & Ratnieks, 2006). These studies show that normative behaviours are not exclusively human and can favour the evolution of conformity. We thus suggest that normative conformity deserves better attention.

1. 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 informational 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. To improve your chances of survival you should stick with the larger group, i.e., copy the majority (Cresswell & Quinn, 2011).

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). 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 can only thrive when behaviours are strategic complements, or non-strategic. In both cases, social information allows inferring which behaviour increases fitness. While usually we consider informational conformity as including only non-strategic settings, we suggest that in effect it should also include the case of strategic complements without punishment.

1. Information acquisition, the value of observations, and memory

Information acquisition is still largely idealized in theory. 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 et al., 2019). 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, probably older observations should be discounted in favour of recent ones, since reliance on past observations could cause a 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 mathematical ones. For instance, what function can maintain conformity while satisfying the necessary mathematical properties (a S-shaped probability, symmetric in all behaviours)? These issues remain under-explored for the moment with few exceptions (e.g., Nakahashi et al., 2012; Mesoudi, 2018).

1. Identifying conformity in animals: Rethinking the mathematical definition

The canonical mathematical model for conformity is the sigmoid curve (Fig. 1 red lines) proposed by Boyd & Richerson (1985) in their initial work on conformity and cultural evolution. While this paradigm retains both theoretical convenience and elegance, it may need reconsideration, to match empirical evidence.

First, individual departures from unanimous majorities (close to 0% or 100%, i.e., the extreme left and right of Fig. 1), are much more frequent in real life than what is imbedded into the canonical model. Such occurrences were documented as early as Asch (1955) and have been corroborated in virtually all studies of conformity (e.g., Battesti et al., 2015; Pike & Laland, 2010; Aplin et a., 2017; Danchin et al., 2018). This phenomenon should not be simply brushed off as ‘behavioural mistakes,’ since it could in fact reveal the existence of heterogeneities within populations or major cognitive limitations. In any case, this feature is ubiquitous enough to warrant attention in modelling, if only because ignoring it when testing for conformity could lead to false negatives.

Secondly, in the canonical model individuals remain hesitant to adopt the majority variant as long as this majority is not strongly established (e.g., 51%). It is an issue given that empirical work has shown that conformity can be surprisingly accurate in detecting majorities around 50%, and that the behavioural response to demonstrator frequencies looks more like a step function than a mild sigmoid curve (Aplin et a., 2017; Danchin et al., 2018; and see Fig. 1). Nonetheless, many studies still use this sigmoid curve when testing for conformity empirically (Battesti et al., 2015; Pike & Laland, 2010; Aplin et a., 2017; Smaldino et al., 2018). This may become an issue for studies requiring formal quantitative tests (typically, if they involve 3 or more behaviours), possibly leading to false negatives.

To answer these concerns, we suggest a simple alternative to the current mathematical definition of conformity. This new definition is grounded in empirical observations: a stepwise-linear function, illustrated by the blue curve in figure 1. This function is characterized entirely by two simple parameters: its value at 0% and 100%, and its slope at 50%. The first parameter fixes the degree of copying fidelity when only one behaviour is displayed in the population. The second parameter reveals the accuracy in detecting an ambiguous majority (share close to 50%). This alternative formalism constitutes a closer fit to empirical observations, making it more convenient to identify conformity when it is there.

1. ANIMAL CONFORMITY

(1) Behavioural ecology

Boyd & Richerson’s conformist transmission model attracted a lot of attention in behavioural ecology, the domain of evolutionary sciences that studies the evolution of behaviour. 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 to adopt 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, ~~follows~~ 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, 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 et al., 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 tradition. This is illustrated in Figure 1 where Boyd & Richerson's definition of conformity corresponds to 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 to adopt 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. These are summarized in Table 1. Unfortunately, it appears that all these studies use very different kinds of definition of conformity with only 10 in 39 incorporating the 'disproportionate' component. Thus, the field would benefit from clearer definition and consistent use of the terminology to allow for comparisons between species and studies. More generally, Table 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 et al., 1998; Dukas & Edelstein-Keshet, 1998; Rolland et al., 1998; Dolligez et al., 1999; Barta & Giraldeau, 2001; Brown & Bomberger Brown, 2001; Serrano et al., 2001; Boulinier et al., 2002; Eberhard, 2002; Varela et al., 2007) that are not usually called conformity, despite the fact that such processes can be envisioned as forms of conformity in space.

Similarly, we did not include the vast literature about mate copying as there is a recent review on that topic (Varela et al. 2018). In effect, the reasoning using the Fisher runaway process that we develop in the next section for the origin of social learning and conformity, also applies to mate copying, which ~~that~~ 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 two 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., copy 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. As a matter of fact ~~s~~ , most studies on mate copying use only a single demonstration for practical reasons, thus ~~refraining~~ preventing us from talking ~~of~~ about majority. 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, observer females can considerably increase the quality of their assessment of the local majority and thus can considerably increase their chance to build 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 ~~suggested~~ 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 et al., 2011). However, we are still lacking a general framework by which conformity may have emerged during the course of evolution.

1. CONFORMITY INN 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 (Table 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, there was always a certain number of individuals that 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 increases 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 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.

1. 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; Laland et al., 2011; Danchin et al., 2018; Lachland et al., 2018). 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). According to our hypothesis we can speculate that all our cultural skills (including the most exquisite arts, religions and believes), 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.

1. 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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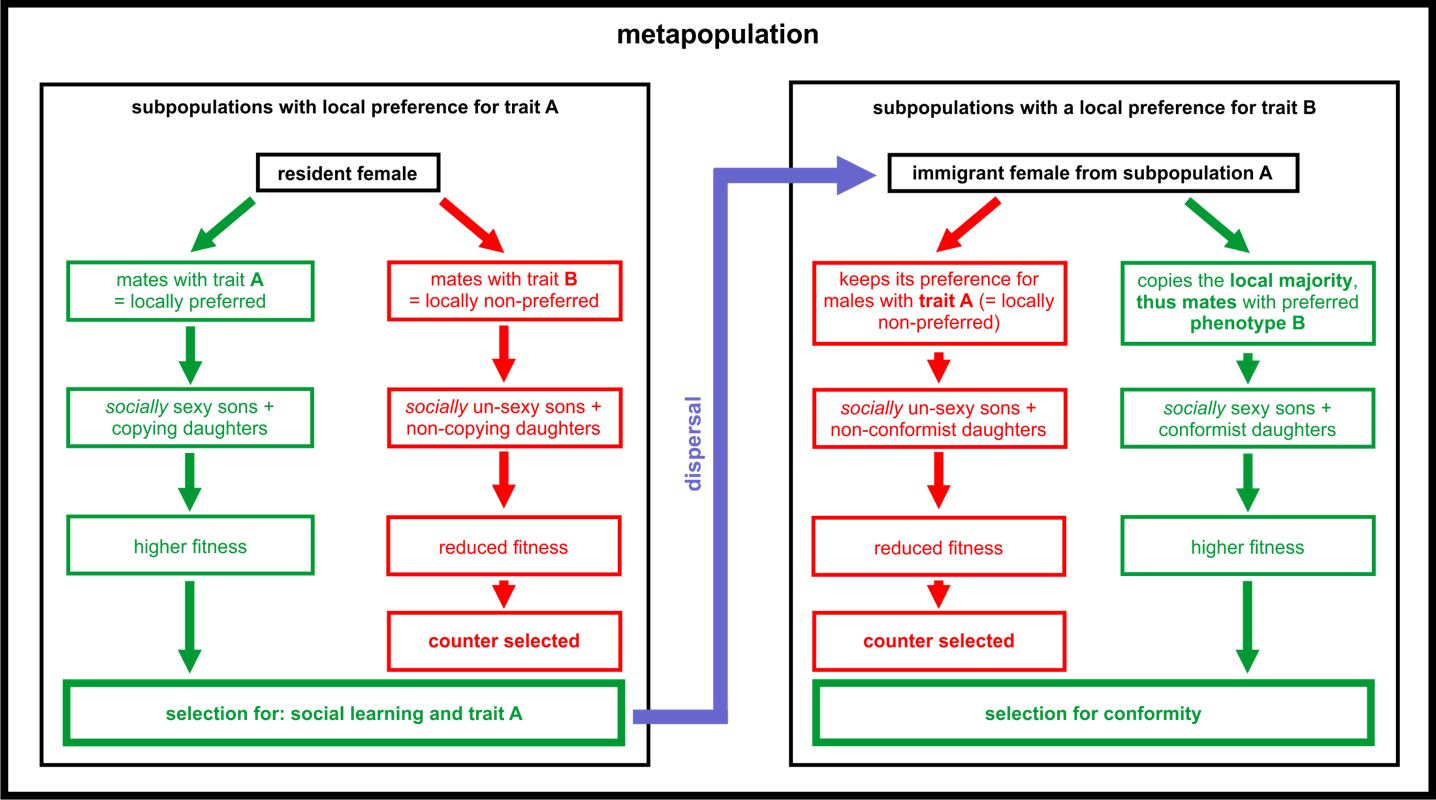
**Table and figures**

**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).

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| --- | --- | --- | --- |
| **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 et al., 2012;  Ayoub et al., 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 et al., 2015 |
| Norway rats (*Rattus norvegicus*) | foraging | “changing one’s behaviour to match that of others” | Jolles et al., 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 et al., 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 et al., 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” | Whiten et al., 2005 ;  Whiten et al., 2007 ;  Hopper et al., 2011 ;  Haun et al., 2012;  Luncz & Boesch, 2014;  Luncz et al., 2014 |



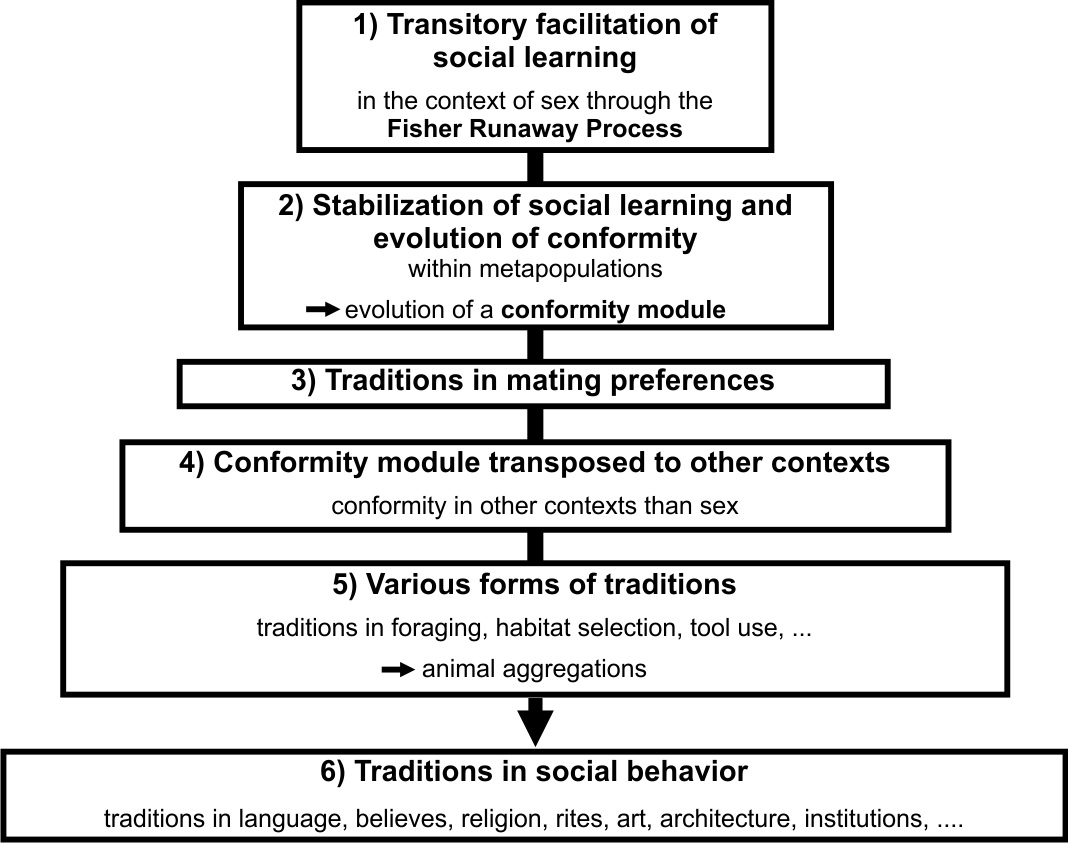
**Figure 1: Defining and formalizing conformity.** Relationship between the proportion of demonstrators adopting one option (X-axis) and that subsequently adopted by observer individuals (Y-axis; in a case with two options). The diagonal black line corresponds to the theoretical baseline of random copying, whereby each observer picks a demonstrator randomly and adopts its behaviour. The grey areas correspond to conformity: observers are *disproportionately likely* to adopt the majority behaviour, i.e., more than under random matching. Contrastingly, the common definition of conformity as 'behaving like, or copying, the majority' covers the grey area, plus the blue area. However, only strategies falling in the grey area can foster the emergence of local traditions, while strategies in the blue area would rapidly converge towards the stable equilibrium at 0.5 and thus do not pertain to conformity. Most models of conformity use the sigmoid curve (red lines) postulated by Boyd & Richerson (1985), which falls entirely in this grey area. The blue line is a response function similar to the one obtained in *Drosophila melanogaster* (Danchin et al., 2018). The yellow-dotted parts of the red lines have almost never been documented in animal and human behaviour as accuracy in copying seems to always hit a ceiling.



**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, and conformity can evolve. Details about simulations can be obtained from authors.

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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.