

## Mate-choice copying can lead to traditions despite weak conformism

**Alexandre Courtiol**  based on peer reviews by **Manuel Sapage** , **Eric Lombaert**  and 1 anonymous reviewer

Déborah Federico, Maximilien Cosme, François-Xavier Dechaume-Moncharmont, Jean-Baptiste Ferdy, Arnaud Pocheville (2026) Gene-Culture Coevolution Favours the Emergence of Traditions in Mate Choice through Conformist Social Learning. *BioRxiv*, ver. 5, peer-reviewed and recommended by Peer Community in Evolutionary Biology.

<https://doi.org/10.1101/2025.09.05.674569>

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Published: 11 February 2026

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Traditions—behavioural practices maintained over time by means of social learning—abound in human populations. They form the basis of group identity and contribute to the dazzling cultural diversity observed in our species. Darwin provides some examples of this in *The Expression of the Emotions in Man and Animals* (1872). On page 216 of the first edition, he wrote “*We Europeans are so accustomed to kissing as a mark of affection, that it might be thought to be innate in mankind; but this is not the case*” and he goes on to list peoples then unfamiliar with the practice (e.g. Fuegians, New Zealanders, Tahitians...) and documents alternative practices that are still unfamiliar to many ‘Europeans’ today (e.g. “*one man striking his own face with the hands or feet of another*”).

As social learning is not exclusive to humans, an observation that did not escape Darwin (Galef, 1996), he would have been pleased, but perhaps not surprised, to learn that traditions have been documented for a menagerie of non-human animals (primates, cetaceans, birds, as well as insects and fishes). For example, the rich song repertoire of certain birds appears to stem from social learning, forming traditions within populations. In the swamp sparrow (*Melospiza georgiana*), some syllables are thought to have endured as cultural phenomena for over 1,000 years (Lachlan et al., 2018).

An important question pertaining to traditions is under which biological conditions they emerge. A well-established theoretical result is that individuals must be *hyperconformist*; that is, individuals must be more likely to express the majority behaviour than the frequency of this behaviour for traditions to emerge. This result is at odds with some experimental results, but as Claidière and Whiten (2012) explained, “*it could also be that the context in which hyperconformity has been [experimentally] investigated is not appropriate*”. Another

possibility is that the models are not appropriate. Many existing theoretical models are simple and adding realism could perhaps expand the conditions under which traditions may form.

This is the argument made by Federico et al. (2026). Inspired by work in *Drosophila* (Danchin et al., 2018), the authors chose to focus on traditions emerging as the result of social learning occurring during mate choice, i.e. *mate-choice copying*. They consider the following situation: males are of type 0 or 1, as determined by a locus with partial heritability; young conformist females learn to prefer the type of male that is most frequently chosen by the subset of adult females they observe. The probability that females conform is set by a parameter  $c$  representing the probability of 'copying fidelity'. Upon reaching maturity, the females express their preference during a single mate choice event, while males can mate multiple times.

In a first simulation model, the authors assume that females always get what they want: having learned that males of type 1 are most chosen (in the sample of the population they were able to observe), a female chooses a male of that type with probability  $c$ . In this situation, the results are similar to those from earlier works: traditions only emerge in contexts that correspond to hyperconformity. Yet, as everyone learns the hard way (and as many have sung in karaokes), *you can't always get what you want*. So, in a second simulation model, the authors introduced realism by considering that mate preferences and mate choice can differ: a female encounters a male of type 1 with a probability that equals the frequency of such a type in the population ( $p_t$ ) and thus our conformist female preferring type 1 now pairs with such a male with a probability  $c$  times  $p_t$ . In this new setting, traditions can emerge even in the absence of hyperconformity!

The argument is subtle but worth grappling with. At the level of mate preference, the authors show that traditions emerge even in settings where conformity is weak, that is when the proportion of females preferring the majority male type is lower than the frequency of such a type. How could this possibly work? Well, the trick is that even in such situations, hyperconformity is to be found at the level of the choice itself and thus at the level of the behaviour being expressed.

Skeptics may downplay this result by arguing that mate-choice copying can only lead to traditions when hyperconformity in behaviour exists and that the behaviour in question is here mate choice. But this view obscures the fact that the trait being socially determined is the mate preference and not the choice itself. For the cultural trait, conformism is truly weak. What makes the evolution of tradition possible under weak conformism is the frequency-dependent selection that female choice exerts on the genetic trait, which in turn impacts the cultural trait. The result is the establishment of "*a positive feedback loop that reinforces the persistence of majority behaviours, thereby promoting the establishment of traditions*" (Federico et al., 2026).

This reinforcing effect is strong enough for traditions to emerge even when females base their preference on the observation of a single mate choice event. A sensitivity analysis of the parameters considered in the model confirms that this result holds for various life histories and demographic settings. Moreover, as the authors remark, the distinction between preferences and expressed choice need not to be restricted to the context of sexual selection but could apply to a wide range of behaviour where individuals compete for resources. The conditions under which learning from a single cultural parent and the type of conformism dynamics that could lead to enduring traditions may not be very restricted after all (*contra* Claidière & Whiten, 2012; Enquist et al., 2010).

Federico et al. (2026)'s models introduce a simple framework that could easily be expanded to study many questions about gene-culture coevolution. This is because the authors parameterised their conformity with individual-level mechanisms in mind. In particular, the shape of the conformity curve emerges from interactions between individuals (instead of being assumed on the population in a top down fashion), which allows for the consideration of other mechanisms that affect such curves. I would be particularly interested in seeing whether it is possible to maintain a general preference for a costly trait (in the current set of assumptions, the male trait is neutral) without exhausting the polymorphism for this trait (see also Kirkpatrick & Dugatkin, 1994). More exciting still would be to study if mate-choice copying would itself be a selected behavior in this context. Whatever the results, sexual selection is likely to remain a fertile ground for the study of gene-culture coevolutionary dynamics and the emergence of traditions. Perhaps this is not surprising; after all, Darwin

had initially intended his work on the expression of emotions as a single chapter in *The Descent of Man, and Selection in Relation to Sex*—his 1871 full-length treatment of sexual selection (Ekman, 2009).

### References:

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## Reviews

### Evaluation round #2

Reviewed by [Eric Lombaert](#) , 10 February 2026

#### Data editors' report

**Editors:** Eric Lombaert & Alexandra Auguste

**Date:** 21/11/2025

#### 1. Data and metadata must be archived and adhere to FAIR guiding principles

[x] Data are in a public repository

[x] Data repository has a persistent identifier (e.g., a DOI)

[x] Data are cited in the manuscript (in data availability statement or similar, as well as in the Literature Cited)

[x] Data repository has a license

[x] All necessary data files are present in the repository

[x] All raw data present

[x] All processed data present

[x] Data are contained in an interoperable format

[x] Tabular data - csv, tsv

Photos -

Videos -

[x] Metadata present (including README file)

[x] Metadata adequate (including README file)

## **2. Archived data corresponds with the data reported in the manuscript**

[x] Variables used in analysis present in the data

[x] The structure of the data presented matches the manuscript (e.g., it is the right size)

## **3. Code and metadata must be archived and adhere to FAIR guiding principles**

[x] Code has a repository

[x] Code repository has a DOI

[x] Code is cited in manuscript

[x] Code repository has a license

[x] Code files are present in the repository

[x] Code is contained in an interoperable format

[x] Metadata present (README file and annotations in code)

[x] Metadata adequate

## **4. Archived code matches the manuscript**

[x] Code is present for all analyses in the manuscript, along with code used to produce figures/tables where appropriate

## **5. Archived code runs with the archived data**

[x] Runs without errors

## **6. Results can be computationally reproduced by running the archived code**

[x] Numeric results (in table or text)

[x] Figures

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### **Comments from the data editor:**

We are grateful to the authors for addressing all the minor concerns raised in the first round of the data and code editing checklist. The data and scripts are now accessible and clearly documented, and are cited

correctly in the manuscript. The codes run smoothly on our computers and produce the same figures.

## Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.1101/2025.09.05.674569>

Version of the preprint: 1

### Authors' reply, 24 January 2026

[Download author's reply](#)

### Decision by **Alexandre Courtiol** , posted 18 November 2025, validated 26 November 2025

Dear Dr Federico and co-authors,

Thank you for sending your preprint to PCI Evol Biol. I evaluated it with the help of two reviewers whose thoughts I hope you will find helpful. Overall, we all enjoyed your manuscript, and provided that a few issues are fixed, I would love to recommend it.

I apologise for the delay. A third evaluation was promised but not delivered, even after an extension was provided, so I decided not to postpone my decision any further. As you will see, this does not seem to have resulted in any significant loss besides your time, since both reviewers did excellent work and picked up on all the key issues that I had noticed, as well as others.

I suggest you consider all the remarks the reviewers made, but I would advise you to focus your effort on two main aspects.

1. One reviewer suggested making an explicit distinction between 'preference copying' and 'choice copying'. I agree with this point. This lack of distinction explains why I struggled with your statement that 'majority exaggeration is not always needed', since this depends on how the majority is defined: by the underlying, non-observable trait (i.e. the preference), as you did, or by what is actually copied (the choice). While this would require some reworking, I believe the paper would benefit greatly from it, as it would further strengthen your argument about the need for explicitly considering the behavioural mechanisms underlying the emergence of traditions.

2. Both reviewers remarked on the unnecessary complexity of having several time steps for juveniles and a survival rate. If the point is to vary the proportion of learners and doers, why not directly fix these? You could directly have one parameter setting the number of juveniles and one setting the number of adults, or you could have a total population size and a frequency of juveniles. If you disagree, please clarify the text to explain why you proceeded as you did.

A series of other (less critical) remarks caught my attention:

- One reviewer wonders why  $K$  does not appear in eq. 2. I think this is because  $K$  influences  $M1$  and  $M2$ , but indeed a brief explanation is called for. Related to that, the reviewer rightly points out that it is not clear how the frequency of encountering type 1 is influenced by former rejections. This is particularly relevant to evaluate the results on the impact of the mating system shown in SI.

- The definition and values used for the mutation rate are both unusual. So perhaps it would be good to provide some explanations. Usually, a mutation leads to a change in a trait and in your case it does not. We understand between the lines that this is to allow for the absence of genetic transmission when  $\mu = 1$ , but still. Also the rate is very high, which calls into question the relevance of results presented in fig 4.

- One reviewer argued that both models are gene-culture models. I think this is a semantic point, since the mutation rate seems to have no effect upon the "cultural model", but I agree that the presence of a genetic

trait in the model could be seen as problematic by some. See what you think, but perhaps using 'preference copying' and 'choice copying' could circumvent this difficulty.

I have divergent views with one reviewer about a particular point:

- Further modelling simplifications were called for by one of the reviewers (the collapse of the parameters  $n_{\text{obs}}$  and  $c$ ) in view of allowing the full analytical study of the model.

While I see the point, I am not sure if this would be straightforward. It would also transform the paper into something substantially different. I personally see the merit in establishing simple simulation models that others can build upon, regardless of their analytical skills; and I think your paper is a perfect example for this. Tackling the simplifications about the juvenile stage discussed above seem to me more important.

The reviewers did not comment on it, but I found the SI results interesting, so I wondered if you could summarise them briefly in the main text. Up to you.

The reviewers also provided a list of minor and constructive points, which I think would help improve the manuscript even further. I also have my own list of minor comments:

- Line 91, before "In this theoretical study", I would start a new paragraph for emphasis sake. Whether you want to merge the next paragraph to that new one is something I have no clear opinion about.
- Line 136: "offspring being randomly distributed": this is unclear since one could think it applies to the trait they carry. I think you meant that the number of offspring is a multinomial draw with equal probability or something along this line. Please clarify.
- Line 204: make it clear that the sampling of the different males occurs during the same (unique since adult) time step.
- Line 260-262: weird phrasing I think. Make it clear that you checked and that it is valid. (We do not validate things by comparing, we check whether things are valid or not by comparing).
- Line 303-313: I got bogged down. Do you look at how long the trait at step 100 continues to remain dominant, or do you wait until after step 100 for something to emerge and then count from that point. You seem to say both. I guess one is for setting the threshold and the other for applying the threshold, but it is not crystal clear.
- Fig 3: traditions in the top row seem to last longer than the corresponding box plot suggests (at  $c = 0.7$ , it seems nothing emerges for more than 10 times steps or so...
- Line 405: weird phrasing, I am not sure you can test modeling with a parameter...
- Line 455: I would write: "Kirkpatrick and Dugatkin questioned..." and before "for example", I would end the sentence and start a new one: "The same applies to our model. For example, the coevolution we observed cannot be attributed"... See if you prefer that or not.
- Line 562: you should drop the ".git" I think.
- Line 645: unlimited yes, but only from the female perspective. For males there is a clear limit in their mating rate. So please rephrase.
- References: there are a few inconsistencies. Some of the articles you cite have capitalised each word in the title, others not. I would only capitalise each word of book titles and book chapter titles. Some abbreviated names are followed by a "." others not. E.g., we have both Kevin N Laland and Kevin N. Laland. You also have a few "et al." that could be expanded to give people due credits.
- Line 798: I doubt that the publisher of Fisher in 1915 was a digital library.

Alexandre Courtiol

## **Reviewed by anonymous reviewer 1, 07 October 2025**

The authors describe a gene-culture coevolutionary simulation of female mate choice and examine the emergence of traditions. They find that a "gene-culture" model produces traditions more readily than does a "cultural" model. Overall I like the manuscript and I think the authors have found a neat result. However, there are a few features of the model that are a bit over-wrought and can be simplified. In addition, the interpretation of the model is a little off in places, one of which is quite important. I'll describe my concerns in more details below.

#### The definition of conformity

On line 118 the authors define conformity as follows: “individuals are considered conformists if they can learn to prefer the behaviour they observe most frequently”. This is fine (people can define things how they want), however, on this basis they then call individuals learning to \*perform\* the behavior they observe most frequently “choice” and not conformity. This is problematic because the conformity literature as a whole blends these two definitions (often in a confusing way) and while the authors are free to define conformity as they wish, picking copying preferences as being “conformity” while copying behaviors becomes something else just adds to the confusion.

I'd suggest making clear both are often considered conformity elsewhere and distinguish them as “preference copying” and “behavior copying”. Emphasizing the difference between preference copying and behavior copying adds to the importance of the manuscript in my opinion. The recent Morgan/vanLeeuwen review of conformist transmission highlighted this as one area that specifically needed more theory (c.f. section Future Directions: Theory).

Separately, in place of a strict conformist transmission definition, the authors define “majority exaggeration”. This is fine. However, on lines 227-229 they state “For each parameter set, we examined whether the emerging conformity curve showed the presence or absence of ‘majority exaggeration’ – that is, a disproportionate tendency to copy the majority”. However, in their “cultural” model the curves always display a mix of conformist exaggeration and anti-conformist under-responding, so I can't fully comprehend how they are defining the presence of exaggeration.

#### The notion of gene-culture interactions

In my opinion both models are gene-culture models. The only time this is not the case is when mutation = 0.5 as now cultural evolution can no longer interact with genetic change. The main difference is that the “cultural” model is a model in which preferences are copied, and the “gene-culture” model is a model in which behaviors are copied. I think this is an important difference, and the model descriptions and naming should be revised accordingly.

#### Model overcomplications

The model includes probabilities  $s$  (juvenile survival) and  $a$  (juvenile progression to adulthood), but why have these at all? They don't do anything or have any impact on the results. It would be far simpler to just have all juveniles survive and grow up (i.e.  $a=s=1$ ) and just leave it at that.

The variable adolescence period creates further oddities when it turns out the number of adults is therefore not constant and  $n_{obs}$  may exceed the adult population size. Again, this is a needless complication. Just keep  $N$ ,  $N_{adults}$  and  $N_{juveniles}$  all constant within a simulation unless there are clear reasons not to do so.

Cultural transmission fidelity is affected by two parameters,  $n_{obs}$  and  $c$ . However, they never act separately and so their combined effect is all that matters. As such, they should just be reduced to a single parameter that captures the effects of both.

Figure 2 is by far the most important figure in the paper. In fact, virtually all of section 2.3 can be predicted simply by looking at figure 2 and so the additional simulations that seek to detect traditions are unnecessary. Fig 2a shows that with preference copying the frequency of the preference will converge to an intermediate frequency determined by transmission fidelity. This is like the curve detected in the Danchin fly work. As in that work the resulting tradition can be unstable, flipping between the two options depending on the fidelity of transmission (the authors can probably analytically derive the expected tradition length between flips from their model assumptions). Fig 2b shows that with behavior copying the population will tend to converge on total dominance by one preference. There is not much need to do any more than simply describing the implications of these results – simulation them in addition is needless complexity.

To my surprise, Fig 3 lower-left panel violates this expectation because behavior copying does not drive the preference to fixation. But this is because the authors assume a truly staggering genetic mutation rate of 0.4. This is so far beyond the realm of biological plausibility that I don't think there's much benefit to considering it. In reality mutation rates are much lower, even a value of 0.01 is high (though often used in simulations for computational expediency). Similarly the authors consider a mutation rate of 0 which is not very informative. A more sensible range of values might be 0.1 (high, but possibly acceptable at a stretch), 0.01, 0.001 (you could add 0.0001 too, though that might just approximate 0 given the population size).

Minor points:

lines 58-59, the authors should briefly spell out why mate choice copying is a promising context.

line 91, the opening “-,” is odd, the comma should probably be removed.

lines 139-146, this section should make immediately clear that only the male trait is genetic, while the female preference is a culturally learned trait and their mating choice is an expressed behavior.

Throughout, the authors model raises the general question of “is a tradition still a tradition if it is itself culturally transmitted, but this transmission is backed up by genetic change such that no other option is really available?”. There isn't really a right answer to this. However, many papers assume that cultural traditions are arbitrary/optional, but that's not always the case in the authors behavior-copying model. The authors might want to hint at this issue in the discussion.

Title and abstract

Does the title clearly reflect the content of the article?  Yes,  No (please explain),  I don't know

Does the abstract present the main findings of the study?  Yes,  No (please explain),  I don't know

Introduction

Are the research questions/hypotheses/predictions clearly presented?  Yes,  No (please explain),  I don't know

Does the introduction build on relevant research in the field?  Yes,  No (please explain),  I don't know

A quick skim of the reference list indicates the authors may wish to read some of the recent work on conformist transmission by Kaleda Denton. In addition, the following two papers may be useful:

Yan, M., Mathew, S., & Boyd, R. (2023). “Doing what others do” does not stabilize continuous norms. *PNAS Nexus*. <https://doi.org/10.1093/pnasnexus/pgad054>

Manning, M. L., Thompson, B., & Morgan, T. J. H. (2024). Norm reinforcement, not conformity or environmental factors, is predicted to sustain cultural variation. *Evolutionary Human Sciences*, 6, e49. <https://doi.org/10.1017/ehs.2024.23>

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers?  Yes,  No (please explain),  I don't know

The method description is sufficiently detailed, but the model itself it overly complex. See comments above.

If applicable (for empirical studies), are sample sizes are clearly justified?  Yes,  No (please explain),  I don't know

Are the methods and statistical analyses appropriate and well described?  Yes,  No (please explain),  I don't know

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)?  Yes,  No (please explain),  I don't know

Are the results described and interpreted correctly?  Yes,  No (please explain),  I don't know  
See my comments above.

#### Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument?  Yes,  No (please explain),  I don't know

Are the conclusions adequately supported by the results (without overstating the implications of the findings)?  
 Yes,  No (please explain),  I don't know

### Reviewed by **Manuel Sapage** , 03 October 2025

In this study, the authors created a model to study the role of conformism in the maintenance of traditions in female acquired preference for a binary male trait through mate-choice copying. This study explores cases where females have access to both types of males independently of their frequency in the population – assuming no fixation (Cultural Model), and when female access to males are dependent to their proportion in the population (Gene-Culture Model).

Overall, I enjoyed reading the manuscript. The text is well written, and I enjoyed the flow of the manuscript. This is a case where the methods work well coupled with the results and I enjoyed reading the discussion as well. In particular, I was happy to see the comparison between this work and Kirkpatrick and Dugatkin's paper and the Evolution of Copying itself in the discussion because I was precisely thinking about these two points when reading the results.

I have listed my comments below. Most of them are minor but I have two major ones regarding the model itself (represented by asterisks \*). These major comments are regarding parameters that have been tested for robustness so I don't think they have an effect on the results, is just the conceptual side of the model that lacks a bit more explanation to clarify the reader on why the model was built the way it was.

#### Comments:

Lines 43-46: I think here is a good opportunity to enumerate the 5 criteria that Danchin et al (citation #26) proposes for the definition of culture, given that you don't have a citation for this statement.

Line 150-151: If I understand correctly, even if there is a mutation, the individual gets a 50% chance to mutate into the same allele they already have. In this case the effective mutation rate is  $\mu/2$ . I understand the way it is modelled for  $\mu = 1$  to coincide with the absence of genetic transmission, but please point that out.

\*Line 170: I am curious why you decide to model a probability for juveniles to transition into adulthood if you reset the female preference between time steps. Shouldn't it be better just to force the juveniles into adulthood or eliminate them if they don't survive? You tested  $\alpha$  and it seems robust, I just don't see a biological reason to include it in the first place.

Line 177: There is a small debate on whether this behaviour should be called "mate-choice copying" or "mate copying" (<https://doi.org/10.1093/beheco/araa076>). While I don't think this debate is relevant here, in line 62 you introduced the term "mate choice copying" (without hyphen) and in line 519-520 you used "mate-choice copying" (with hyphen). I suggest changing the terms to either "mate-choice copying" or "mate copying" for consistency.

\*Line 200-201: Is the probability of each type of male to be sampled equal to the frequency in the population at time  $t$ ? If that is the case, you are either assuming a large  $K$ , or you assume that the rejected males can be resampled by the female. On the other hand, you state in line 205 that there is a possibility to end the male pool. In your model, females learn through an hypergeometric model (equation 2) and I imagine that  $K$  is relevant here. From what I can understand, the effects of  $K$  in your model only affects the copying part of the female preference and not the sequential choice itself, am I correct? Please add a small explanation for this point.

Figure 2: Please add the description for nmat

Lines 278-280: Here you say that  $nobs \leq 2$  is single-copying. Shouldn't it be  $nobs < 2$ ?

Line 364: Please change "increases" to "increase"

Supplementary materials:

Lines 572, 576, 582 – Please lowercase "Figure" for consistency

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Title and abstract

Does the title clearly reflect the content of the article? [X] Yes, [ ] No (please explain), [ ] I don't know

Does the abstract present the main findings of the study? [X] Yes, [ ] No (please explain), [ ] I don't know

Introduction

Are the research questions/hypotheses/predictions clearly presented? [X] Yes, [ ] No (please explain), [ ] I don't know

Does the introduction build on relevant research in the field? [X] Yes, [ ] No (please explain), [ ] I don't know

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers? [X] Yes, [ ] No (please explain), [ ] I don't know

Are the methods and statistical analyses appropriate and well described? [X] Yes, [ ] No (please explain), [ ] I don't know

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? [ ] Yes, [ ] No (please explain), [ ] I don't know – I do not think this point is applicable here.

Are the results described and interpreted correctly? [X] Yes, [ ] No (please explain), [ ] I don't know

Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [X] Yes, [ ] No (please explain), [ ] I don't know

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? [X] Yes, [ ] No (please explain), [ ] I don't know