**Response to Reviewers**

**Ref:** TPB\_2018\_86  
**Title:** Vertical and oblique cultural transmission fluctuating in time and space  
**Journal:** Theoretical Population Biology

**Date:** 4 November, 2018

Dear Editorial Office,

Attached please find the modified manuscript, “Vertical and oblique cultural transmission fluctuating in time and space”. We believe that our responses have taken care of all the comments and suggestions from both reviewers. Briefly:

1. We clarified our hypothesis (line 61) and model (lines 65, 72, 76)
2. We emphasized that this work is a generalization of Ram et al. 2018 (lines 47, 65)
3. We provided additional examples for the considered traits (line 68) and mechanism for fluctuating transmission (line 43)
4. We added several new paragraphs to the Discussion, including citations for the manuscripts suggested by Reviewer #2:
   * Line 313, speculating about the evolution of the transmission rate in a heterogeneous spatial model;
   * Line 321, describing the model and results of Bisin and Verdier 2001 and how they relate to our work;
   * Line 336, relating our results to Rogers’ paradox;
   * Line 379, providing more detail on our choice to model migration after transmission.
5. We fixed typos in Figure 5 and line 146.

Please find below a point-by-point response to the reviewers comments.

Yours sincerely,

Yoav Ram, Uri Liberman, and Marcus W. Feldman

**Reviewer 1**  
This paper provides an interesting exploration of the role of mode of transmission in a uniparental model of cultural evolution. The models presented are a straightforward elaboration of previous work on the effect of fluctuating selection on the evolution of oblique vs. vertical transmission of a cultural trait.  In this paper, the authors explore the effect of both fluctuating selection and fluctuating transmission simultaneously.

I believe this paper is an important addition to the literature on transmission mode evolution in cultural evolution, and the the larger literature on modifier theory. The mathematical results are clearly demonstrated and the special cases well chosen. As such, I recommend this paper for publication with some minor revisions, listed below:

* line 137: the text seems to indicate that the distribution of  rho\_t is subject to a constraint P(-1+C<z\_t<D), but there is no equality (I'm assuming this should be "=1.") It wasn't exactly clear to me where this assumption is used in the proof of the stochastic stability results, but it should be fixed.

Correct, we had a typo. We now fixed it in line 146 to be “P(-1+C < z\_t < D)=1”.

* Fluctuations in space: The numerical results show that when migration to and oblique transmission within deme 1 are higher relative to deme 2, then fixation of A is favored.  Can the authors provide some intuition for this result that seems somewhat paradoxical?  As more migrants are received from the deme where B is favored, and these migrants have a better chance of passing B on to the offspring of A individuals, it would seem that A could be at a disadvantage, despite it's being favored by selection. In other words, it seems to me that the response to selection should be greater in deme 2, leading to a higher frequency of B migrants to deme 1.  How is it then that as deme 1 receives more of these migrants, and has a presumably reduced response to selection due to more oblique transmission, that fixation of A is more stable? This could be presented in the discussion section of the paper, but I think it bears acknowledgement.

We thank the reviewer for his critical analysis of Figure 5. There was a typo in the code that generated the figure causing the “A fixation” and “B fixation” labels to swap. We recreated the figure with the correct labels: A fixes when vertical transmission is stronger in deme 1 and migration is higher into deme 2. B fixes when vertical transmission is stronger in deme 2 and migration is higher into deme 1.

* The presentation of the mathematical results is clear, but relies heavily on previous results from Ram et al. 2018.  I think that the discussion could be expanded to contextualize the results from previous sections, and, in effect, provide a verbal summary of the major results in a way that is more comprehensive than the current version.
* We added a new paragraph that speculates how the results from Ram et al. 2018 on the evolution of the transmission rate under temporally fluctuation selection relate to spatially fluctuating selection and transmission, line 313: “The interaction between spatially varying selection and transmission is shown in Figures 6 and 7 to depend on migration in a complex way. However, our two-deme model does not exhibit the kind of complexity seen in Ram et al. (2018), where the period of environmental fluctuation determined whether the vertical transmission rate ρ that maximized the population mean fitness was the same as the evolutionarily stable value. We can speculate that a model with more sub-populations and a more geographically complicated fitness regime might show less predictable relationships between transmission and selection.”
* A verbal summary of our results is given in line 299.

**Reviewer 2**

In *Vertical and oblique cultural transmission fluctuating in time and in space*, the authors investigate the change of frequency of a cultural trait, when selection on this trait and its transmission mode fluctuate. The work is an extension to a previous paper by the same authors (*Evolution of vertical and oblique transmission under fluctuating selection, PNAS*), in which transmission mode did not fluctuate (but evolved).

The paper is clear and well-written. However, there are a few points that need addressing.

1. First, the motivation for the study is not very clear to me. The authors give a few examples in the introduction (l. 36-40) why transmission mode may fluctuate in nature. But these examples show there are causal mechanisms that lead to fluctuations in transmission mode (e.g., stress), which suggest that it may be adaptive (or a constraint).

Why not then look at the evolution of transmission mode as a reaction norm to a variable environment?

Indeed, we suggest in the *Discussion* that an extended model could explore the evolution of plastic transmission modes. We now emphasize this in line 391: “We suggest that the specific mode of oblique transmission can also fluctuate over time, so that individuals can, for example, conform to the frequent phenotype under benign conditions, and prefer a rare phenotype under stressful conditions; more generally, the mode of transmission could be plastic and viewed as a reaction norm to variable environments.”

In short, what is the biological question that the authors seek to answer with their model?

We modified the last paragraph of the introduction to clearly state our hypothesis, line 61: “We suggest that cultural evolution can be affected by environmental changes that cause temporal or spatial variation in either selection or transmission or both, and that such variation has a significant effect of trait polymorphism.”

2. More broadly, I have found the absence of any link with biology in the results section cheerless, making it a dry read. The manuscript would be improved if examples were given throughout. For example:

What type of cultural traits A and B could be?

We added a sentence to *Model and Results* with examples of traits, line 68: “Example traits include foraging and hunting techniques, such as lobtail feeding in humpback whales (Allen et al., 2013) and fruit processing in capuchin monkeys (Barrett et al., 2017), child caring, mating skills, and dancing in human hunter-gatherers (Hewlett and Cavalli-Sforza, 1986), and even canoe design in Polynesia (Rogers and Ehrlich, 2008).”

Why would transmission mode differ between traits, in time and in space?

* We added another example from human culture, line 43: “Hewlett et al. (2011) found that the balance between vertical and non-vertical cultural transmission depends on core cultural values and therefore differs between hunter-gatherers and farmers.”
* This new example expands upon the paragraph that cites different examples of mechanisms that lead to fluctuations in transmission rates (line 36).

3. The introduction and discussion are frustratingly cursory. In order to reveal the novelty and relevance of the model’s results (which are still unclear to me), the authors should give greater context to their study.

We added several paragraphs to the *Discussion*:

* Line 313, speculating about the evolution of the transmission rate in a heterogeneous spatial model;
* Line 321, describing the model and results of Bisin and Verdier 2001 and how they relate to our work;
* Line 336, relating our results to Rogers’ paradox;
* Line 379, providing more detail on our choice to model migration after transmission.

4. In particular, there have been a few studies on the influence of transmission mode on cultural polymorphism (which is the only point the authors really discuss, l. 290-302): e.g.,

1) *The Economics of Cultural Transmission and the Dynamics of Preferences*(Journal of Economic Theory, 2001);

2) *Invasion fitness for gene-culture co-evolution in family-structured populations and an application to cumulative culture under vertical transmission*(Theoretical Population Biology, 2017).

The authors should place their results within the backdrop of these papers (and other relevant literature).

* We have added a paragraph to the *Discussion* that describes the model and results of Bisin and Verdier 2001 and how they relate to our work, line 321: “An interesting model with a similar structure was studied by Bisin and Verdier (2001): it included both vertical (i.e. “socialization in the family”) and non-vertical (i.e. “imitation from society”) transmission. They focused on a frequency-dependent transmission mode called cultural substitution, in which a parent invests more in child socialization if the parental trait is rare. Their model (eq. 12) is a continuous- time equivalent of our model (eq. 1) that does not distinguish between horizontal and oblique transmission; considers constant, rather than fluctuating, selection; and includes endogenously fluctuating transmission due to changes in trait frequency. They have found that under some selection schemes, in which parents choose how many offspring to produce, either an unstable polymorphism (Proposition 4) or a sta- ble polymorphism (Proposition 5) exists, depending on the costs associated with the transmission mode. Furthermore, in the absence of selection trait polymorphism is neutral in our model (set s = 0 in eq. 1), but Bisin and Verdier (2001) have found that frequency-dependent transmission leads to a globally stable polymorphism (Proposition 1).”
* We have added a new paragraph to the *Discussion* that relates our results to the effect of population structure to Rogers’ paradox and cumulative culture, in which we describe the model and results of Mullon and Lehmann, 2017, line 355: “Mullon et al. (2017) have also studied a model of individual and social learning that includes both vertical and oblique transmission in a cumulative culture setting. Their results show that the effect of vertical transmission on maintenance of individual learning is stronger if vertical transmission is more efficient than oblique transmission, i.e. “if offspring learn better from relatives, or if parents devote more teaching effort towards offspring”.”

5. For the model of fluctuations in space, the authors assume that oblique transmission occur before dispersal. This seems relatively less interesting to the case when oblique transmission occurs after dispersal. The authors should discuss this possibility and how it would change their results.

1. We added a paragraph to the *Discussion* about our choice for transmission to occur before dispersal, which is necessary for modeling vertical transmission, line 379: “Our spatial model (eqs. 18-19) assumes migration by sub-adults, or more specifically, that migration follows cultural transmission, which occurs at the native deme. This is a necessary assumption for modeling vertical transmission, which cannot occur after offspring migrate out of their native deme, leaving their parents behind. Other authors have taken a different approach when focusing on oblique transmission: for example, Kobayashi and Wakano (2012) assumed migration by juveniles, followed by a combination of individual and social learning at the new deme. Further work could investigate the evolution of vertical vs. horizontal transmission, in which case migration could occur before transmission, rather than after.”
2. We added a remark that clarifies that transmission occurs between adults and juveniles, line 72: “Phenotypes are transmitted from adults to juveniles: vertically from parent to offspring with probability ρ, or obliquely from random adults to offspring with probability 1 – ρ.”

6. Also, there have been several studies of gene-culture coevolution in spatially structured populations, sometime with spatial and environmental heterogeneity that also look at the effect of dispersal on local adaptation (genetic or cultural load), e.g.,

1) *EVOLUTION OF SOCIAL VERSUS INDIVIDUAL LEARNING IN AN INFINITE ISLAND MODEL*(Evolution, 2011);

2) *Inclusive fitness analysis of cumulative cultural evolution in an island-structured population*(Theoretical Population Biology, 2017)  
Again, these works should be referred to and contrasted with the present study.

We thank the reviewer for pointing out these studies. We have added a new paragraph to the *Discussion* that cites these studies and relates our results to the effect of population structure to Rogers’ paradox and cumulative culture, line 336: “An important topic in cultural evolution is the evolutionary dilemma known as Rogers’ paradox (Rogers, 1988), which is similar to the problem of the maintenance of co- operation: social learners (aka cheaters) benefit from new cultural traits invented by individual learners (aka cooperators) without paying the cost associated with individual learning. Several authors used population structure to help explain the maintenance of individual learning in this scenario, paralleling the use of population structure for explaining the maintenance of cooperation. For example, Kobayashi and Wakano (2012) modeled both individual learning and social learning via oblique transmission in an infinite island model. Their results show that spatial subdivision favors individual learning over social learning. Maintenance of individual learning is also crucial for cumulative culture, in which cultural innovations made by individual learning are transmitted and accumulated via social learning. Similarly to the effect of cheating in public goods games, social learning can cause the collapse of cumulative culture (Wakano and Miura, 2014). To resolve this dilemma, Ohtsuki et al. (2017) modeled individual and social learning in a structured population, but allowed social learning to be at least partially vertical, rather than completely horizontal or oblique. They have demonstrated that if kin-selection has a significant effect on the dynamics, then increases in inclusive fitness due to vertical transmission can negate the cost of individual learning, at least to some extent, and allow for high levels of cumulative culture to evolve. Mullon et al. (2017) have also studied a model of individual and social learning that includes both vertical and oblique transmission in a cumulative culture setting. Their results show that the effect of vertical transmission on maintenance of individual learning is stronger if vertical transmission is more efficient than oblique transmission, i.e. “if offspring learn better from relatives, or if parents devote more teaching effort towards offspring”. Following our hypothesis that the transmission mode fluctuates over time and space, we suggest that such fluctuations could facilitate the maintenance of individual learning, and therefore cultural accumulation: when vertical transmission is high, innovation by individual learning will be common due to increased inclusive fitness; when oblique transmission is high, new cultural traits will quickly spread via social learning.”

Minor point:

Eq. 1, please refer to eq. 2 of *Evolution of vertical and oblique transmission under fluctuating selection, PNAS,*in whichit is more transparent. It wasn’t immediately clear to me when selection took place until I looked at the second line of eq. 2 of the PNAS paper.

1. We modified the *Introduction* to make it more clear that this work is a generalization of Ram et al. 2018, see line 47: “We previously analyzes a model (Ram et al., 2018) in which individuals learn a cultural trait from their parents with probability ρ (vertical transmission), and from adults in the parental generation with probability 1 − ρ (oblique transmission; see Figure 1). Here, we generalize this model to allow for the vertical transmission rate ρ to fluctuate over time or space.”
2. We replaced eq. 1 with eq. 2 from Ram et al., 2018 (with wA=1+s and wB=1), see line 76.
3. We added a remark at the beginning of *Model and Results* that our model follows and extends Ram et al 2018.
4. We added a remark to *Model and Results* that clarifies when selection takes place, line 65: “we consider a very large population whose members are characterized by a single dichotomous cultural trait with phenotypes A and B that determine the reproductive success of adults, with fitness values wA = 1 + s and wB = 1, respectively.”
5. We added a remark to *Model and Results* that clarifies that transmission occurs between adults and juveniles, line 72: “Phenotypes are transmitted from adults to juveniles: vertically from parent to offspring with probability ρ, or obliquely from random adults to offspring with probability 1 – ρ.”