

See my notes below (I know you love R, but this is quite tedious for both of us)
The only major things to change are: end of intro - I think we can answer that there need not be copying in apes, but we cannot say that CC needs copying. Also, we need a new Figure 1 - the WOW Whiten figure. Will is

Culture in oranzees

Alberto Acerbi^{a,1}, William Snyder^b, and Claudio Tennie^b

^aCentre for Culture and Evolution, Department of Life Sciences, Brunel University London, Uxbridge, UB8 3PH, United Kingdom; ^bFaculty of Science, Department for early prehistory and quaternary ecology, University of Tübingen, Schloß Hohentuebingen, Burgsteige 11, 72070, Tübingen, Germany

This manuscript was compiled on November 22, 2019

Please provide an abstract of no more than 250 words in a single paragraph. Abstracts should explain to the general reader the major contributions of the article. References in the abstract must be cited in full within the abstract itself and cited in the text.

one | two | optional | optional | optional

Culture, the transmission of knowledge, technologies, and beliefs from individual to individual, and from one generation to the other, is key to explain the extraordinary ecological success of our species (1). Which cognitive abilities underpin humans cultural capacities, and how these abilities affect the evolution of culture itself are among the most pressing question of evolutionary human science.

Many other species, besides humans, are able to transmit information socially, from primates (3) to fish (4) and even insects (5). Differently from these species, however, humans create cumulative culture. While there are various definitions of cumulative culture (6), some of its characteristics are broadly accepted. Cumulative culture requires the accumulation of cultural traits (more cultural traits are present at time t than at time $t-1$), their improvement (cultural traits at time t are more effective than traits at time $t-1$), and ratcheting (the innovation of cultural traits at time t depends on the presence of other traits at time $t-1$). Refs?

Not all human cultural traditions need to be supported by faithful copying (7), but a species capable of cumulative culture needs to be able to transmit and preserve accurately new information. Experiments have indeed shown that humans are capable of that, and they routinely do it. More controversial is the claim that other species do, especially outside of experimental scenarios built on purpose. Claims regarding the existence of animal cultures based on faithful copying raise a puzzling question: if other species can and do copy, why they did not develop comparable cumulative cultures? There are only two possible answer to this question. Either they do not copy, or faithful social learning does not automatically lead to cumulative culture. copying

Besides experiments, satisfying answers to this question should come from observations of real-life instances of culture among non-human species. Primatologists have claimed the existence of copying-based cultures from observations of wild populations. (8) examined the population-level distribution of behavioral traits in populations of chimpanzees at six sites, and it argued that this distribution proved the existence of different cultures in these populations. While we can not replicate wild observations changing their parameters, or re-run history to see the likelihood of a particular outcome, modelling can help to assess the robustness of such claims.

We developed an individual-based model to assess whether the patterns observed in the wild and described in (8) actually warrant the existence of culture supported by faithful copying abilities. We reproduced, in our model, several details of the original study, including realistic demographic and spatial

features, and effects of ecological availability and genetic predisposition, to investigate whether an equivalent distribution of behavioral traits could emerge in the simulated populations. While our simulated species, *oranzees*, can be influenced by social cues present in the environment (as widespread in the animal kingdom), we did not model any high-fidelity social learning mechanisms. excluded copying

Our results show that, under realistic values of the main parameters, we can reproduce the distribution of behavioral traits found in (8). In other words, as oranzees can and do show cultural patterns resembling wild ape patterns, this is proof that such patterns cannot be counted as evidence that copying takes place. This provides an answer to the puzzling question we presented above: copying is necessary and leads to cumulative culture, but ape cultures are not based on it. without any copying required must have taken place

Materials and methods

We built an individual-based model that reproduces a world inhabited by six populations of “*oranzees*”, an hypothetical ape species. The model is space-explicit: the oranzees populations are located at relative positions analogous to the six chimpanzees sites in (8). This is important to determine the genetic predispositions and ecological availabilities associated to their behaviours (see below). Population sizes are also taken from the sites in (8). Following (9), we use data from (10), and we define population sizes as $N = \{20; 42; 49; 76; 50; 95\}$.

Oranzees are subject to an age-dependent birth/death process, broadly inspired by descriptions in (11). A time step t of the simulation represents a month in oranzees' life. From when they are 25 years old ($t = 300$), there is a 1% probability an oranzee will die each month, or they die when they are 60 years old ($t = 720$). The number of individuals in the population is fixed, so each time an oranzee dies is replaced by a newborn. possible

A newborn oranzee does not have any behaviour. Behaviours can be innovated at each time step. The process of innovation is influenced by: (i) the oranzees ‘state’, which depends from the behaviours an individual already possesses, yet show on

Significance Statement

Authors must submit a 120-word maximum statement about the significance of their research paper written at a level understandable to an undergraduate educated scientist outside their field of speciality. The primary goal of the Significance Statement is to explain the relevance of the work in broad context to a broad readership. The Significance Statement appears in the paper itself and is required for all research papers.

Please provide details of author contributions here. XX

Please declare any conflict of interest here. XX

(ii) the frequency of the behaviours already present in the population (“socially-mediated innovation”), and (iii) the genetic propensity and ecological availability associated to the behaviour. At the beginning of the simulations, the populations are randomly initialised with individuals between 0 and 25 years old.

State. In the oranzee world, 64 behaviours are possible. Behaviours are divided in two categories, namely 32 social and 32 food-related behaviours.

In the case of social behaviours, we assume four sub-categories, each with eight possible different behaviours, that serve the same goal. Oranzees’ state is based on how many of the four goals are fulfilled. A goal is considered fulfilled if an oranzee has at least one behaviour out of the eight in the sub-category. An oranzee has a state value of 0.25 if, for example, it has at least one behaviour among the first eight behaviour, and none of the others, and a state value of 1 if there is at least one behaviour in each sub-category. p_{social} , the probability to innovate a social behaviour, is drawn from a normal distribution with mean equal to $1 - \text{state}_{\text{social}}$.

Food-related behaviours are analogously divided in sub-categories, with the differences that there is a variable number of behaviours in each sub-category, and that sub-categories are associated to two different ‘nutrients’, Y and Z . The idea is that individuals need to balance their nutritional intake, so that their optimal diet consist in a roughly equal number of foodstuff for one and the other nutrient. The state, for food-related behaviours, depends on the total amount of food and on the balance between nutrients, and it is calculated as the sum of each sub-category fulfilled (as above, for this happening there needs to be at least one behaviour) minus the difference between the number of sub-categories providing nutrient Y and the number of sub-categories providing nutrient Z . We normalize the state between 0 and 1, and, as above p_{food} is then calculated as $1 - \text{state}_{\text{food}}$. (Further details in SI).

Socially-mediated innovation. At each time step, all oranzees have a probability of innovation for social and food-related behaviours calculated as described above. The specific behaviour an oranzee will innovate may depend both on the frequency of the behaviours already present in the population, and on the ecological availability and genetic propensity associated to the behaviour. A further parameter of the model, S , controls the probability that each innovation is socially-mediated. When an innovation is socially-mediated, the probability of innovating each behaviour B_i is weighted by its proportional instances in the population, among the behaviours of the same category, so that common behaviours are more likely to be innovated.

When the innovation is not socially-mediated, the probability of innovating each behaviour is random. Only one behaviour per category can be innovated at each time step.

Genetic propensity and ecological availability. The behaviour selected in the previous step is actually innovated according to its genetic propensity and, in case of food-related behaviours, ecological availability.

Genetic propensity is a probability $p_g(0, 1)$, assigned independently to each of the 64 behaviours. A parameter of the model, α_g , determines the probability that the genetic

propensity of each behaviour is equal for all the six populations or is different.

If it is equal, p_g is randomly drawn. If different, we assign it using a geographical gradient. We choose a random point and calculate its distance to each population. Distances are then transformed to p_g by rescaling them between 0 and 1, so that for the farther site $p_g = 0$ i.e. the associated behaviour will be impossible to express (see SI). Notice that $\alpha_g = 0$ does not mean that there are not genetic influences on the behaviours, but that there are no differences between the populations with this respect.

Ecological availability is a probability $p_e(0, 1)$ that represents the likelihood of finding a resource, or its nutritional value, in each site. Ecological availability is assigned only to food-related behaviours, and it is calculated in the same way of p_g , using the parameter α_e to determine the probability of ecological availability being different in the six populations.

Model’s output. We run simulation for $t_{\text{max}} = 6000$ (corresponding to 500 years of oranzee-time). For each simulation, following (8), we classify each behaviour, in each population, as:

- *customary*: a behaviour observed in over 50% of individuals in at least one age class (see SI for how age classes are defined in our model).
- *habitual*: a behaviour observed in at least two individuals across the population.
- *present*: a behaviour observed in at least one individual across the population.
- *absent*: a behaviour never observed in the population.
- *ecological explanations* is a behaviour that is absent because of local ecological features (i.e., in our model, associated to $p_e = 0$).

Notice the last category in (8) (*unknown*, i.e. “the behaviour has not been recorded, but this may be due to inadequacy of relevant observational opportunities”) does not apply in our case.

Finally, we calculate the same “patterns” described in (8):

- *A*: patterns absent at no site.
- *B*: patterns not achieving habitual frequencies at any site.
- *C*: patterns for which any absence can be explained by local ecological factors.
- *D*: patterns customary or habitual at some sites yet absent at others, with no ecological explanation, i.e. the behaviours defined as “cultural”.

Results Start with their "Wow" pictures - as figure 1

We are particularly interested in the realistic parameter conditions of moderate to high environmental variability ($\alpha_e = (0.5, 1)$) and zero to moderate genetic differences ($\alpha_g = (0, 0.5)$). We run 20 simulations for each combination (for a total of 600 runs). For all, innovation is socially-mediated ($S = 1$). The results show that various combinations of parameters produces a number of cultural behaviours (pattern *D*)

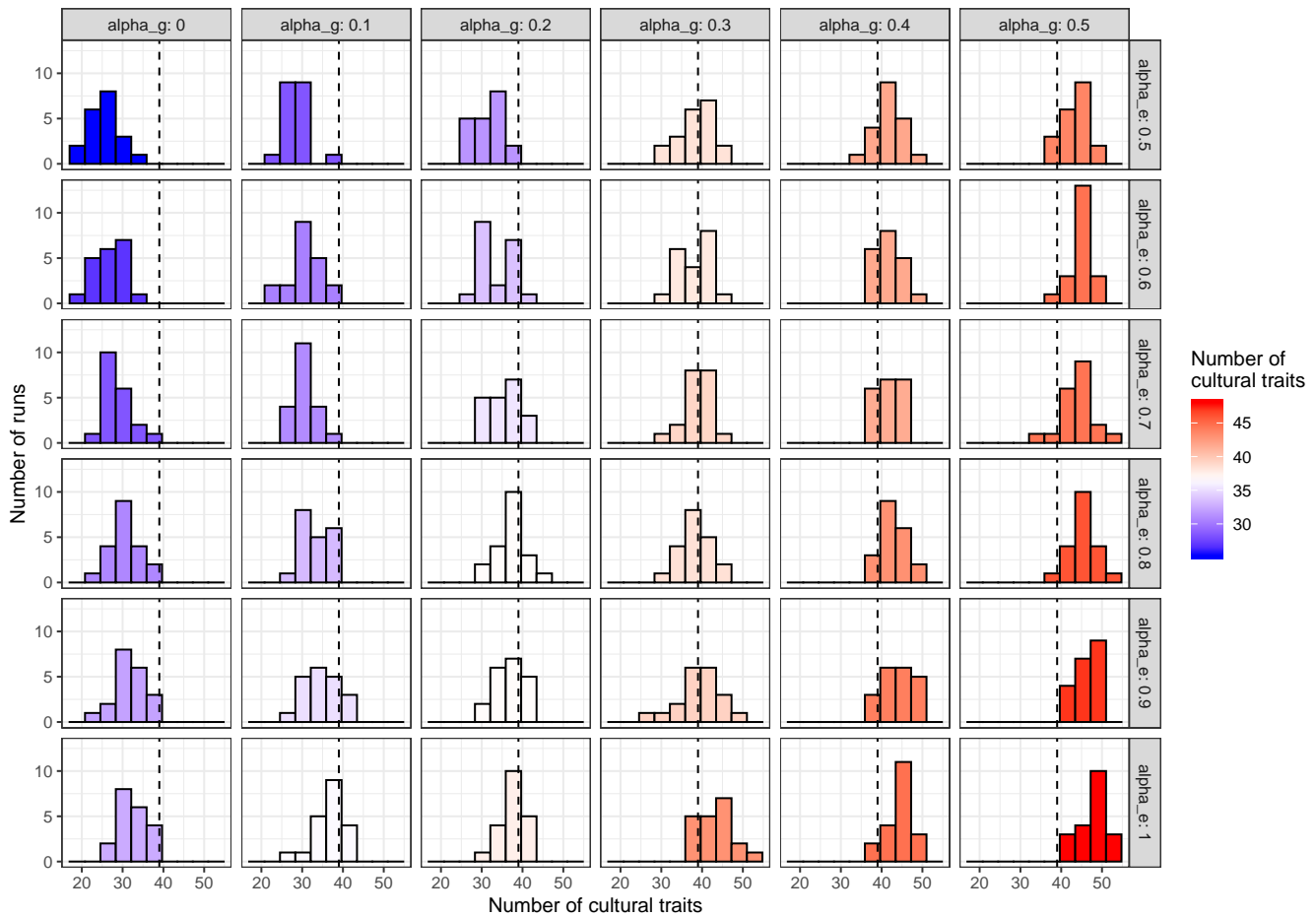


Fig. 1. Cultural traits in oranzees, varying ecological and genetic diversity. Red colour indicates simulation runs that produced more than 38 cultural behaviours; blue colour indicates simulation runs that produces less than 38 cultural behaviours. For all simulations, $S = 1$, α_e and $\alpha_g = 0$ as indicated in the plot. $N = 20$ runs for each parameters combination.

consistent with the 38 found in (8), in absence of any explicit copying mechanism implemented (see Figure 1).

We also analyse the effect of the parameter S (proportion of socially-mediated innovations), in three conditions (see Figure 2): (a) no genetic differences and intermediate ecological differences (compare to the high-left angle of Figure 1, where with $S = 1$ simulations produce less than 38 cultural behaviours), (b) good match with (8), and (c) intermediate genetic differences and high ecological differences (compare to the low-right angle of Figure 1, where with $S = 1$ simulations produce more than 38 cultural behaviours). As expected, decreasing S , decreases the number of cultural behaviours. Conditions where, with $S = 1$, there were more than 38 cultural behaviours could still produce results analogous to (8), if not all innovations are socially mediated.

Our results show that our model not only reproduces the number of cultural behaviours (pattern D), but also the number of behaviours classified in the other three patterns (A, B,

C) in (8). Figure 3 show the four patterns produced in one of the conditions for which we have a good match for cultural behaviours ($\alpha_e = 0.8$; $\alpha_g = 0.2$, $S = 1$).

Finally, we run 100 simulations for the same condition where we have a good match for cultural behaviours with (8) ($\alpha_e = 0.8$; $\alpha_g = 0.2$, $S = 1$). In each simulation, we recorded, for each population, the number of behaviours (habitual + customary + present) that are also classified as cultural (see Figure 4). We find a small, but significant correlation between population size and number of cultural traits ($p < 0.00001$, $\rho = 0.2$, $N = 600$).

That is, we find an effect of accumulation relative to population size (similar to IRL XX)

Discussion

TO DO

ACKNOWLEDGMENTS. Please include your acknowledgments here, set in a single paragraph. Please do not include any acknowledgments in the Supporting Information, or anywhere else in the manuscript. XX ERC grant. Mima.

refs are muddled up:

1. Henrich J (2015) *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter* (Princeton University Press, Princeton & Oxford).
2. Boyd R (2017) *A Different Kind of Animal: How Culture Transformed Our Species* (Princeton University Press, Princeton).
3. Whiten A (2000) Primate culture and social learning. *Cognitive Science* 24(3):477–508.
4. Brown C, Laland KN (2003) Social learning in fishes: A review. *Fish and Fisheries* 4(3):280–288.
5. Leadbeater E, Chittka L (2007) Social Learning in Insects

versity Press, London & New York).

8. Whiten A, et al. (1999) Cultures in chimpanzees. *Nature* 399(6737):682–685.

9. Lind J, Lindenfors P (2010) The Number of Cultural Traits Is Correlated with Female Group Size but Not with Male Group Size in Chimpanzee Communities. *PLoS ONE* 5(3). doi:10.1371/journal.pone.0009241.
10. Wrangham BW (2000) Why are male chimpanzees more g

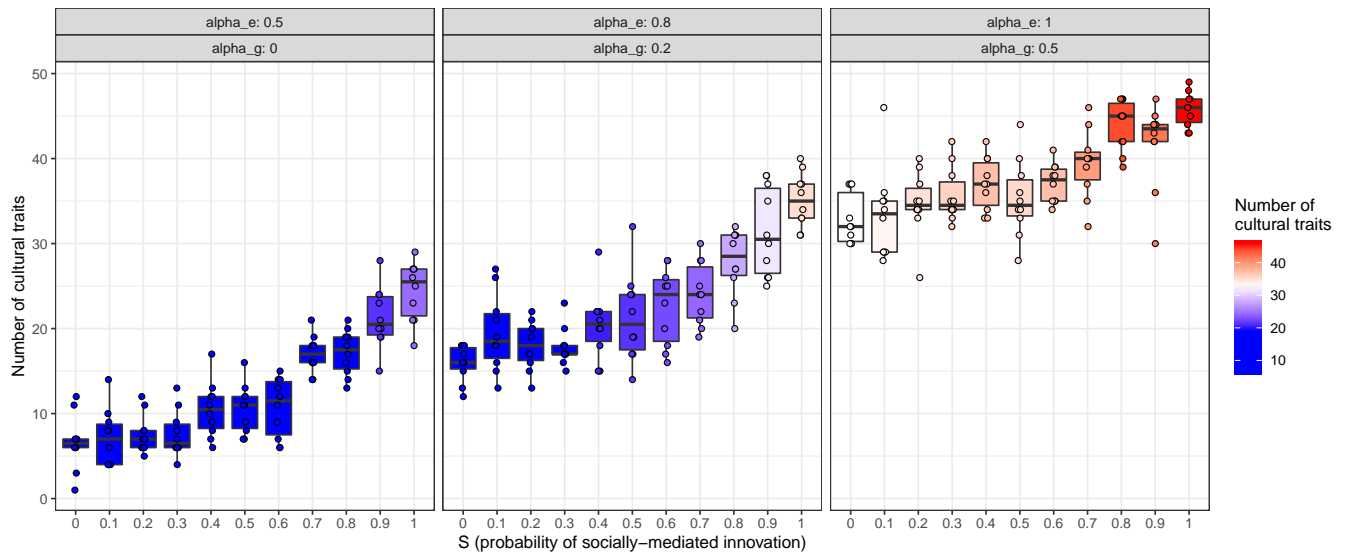


Fig. 2. Cultural traits in oranzees, varying the probability of socially-mediated innovations. Red colour indicates simulation runs that produced more than 38 cultural behaviours; blue colour indicates simulation runs that produces less than 38 cultural behaviours. S , α_e and $\alpha_g = 0$ as indicated in the plot. $N = 10$ runs for each parameters combination.

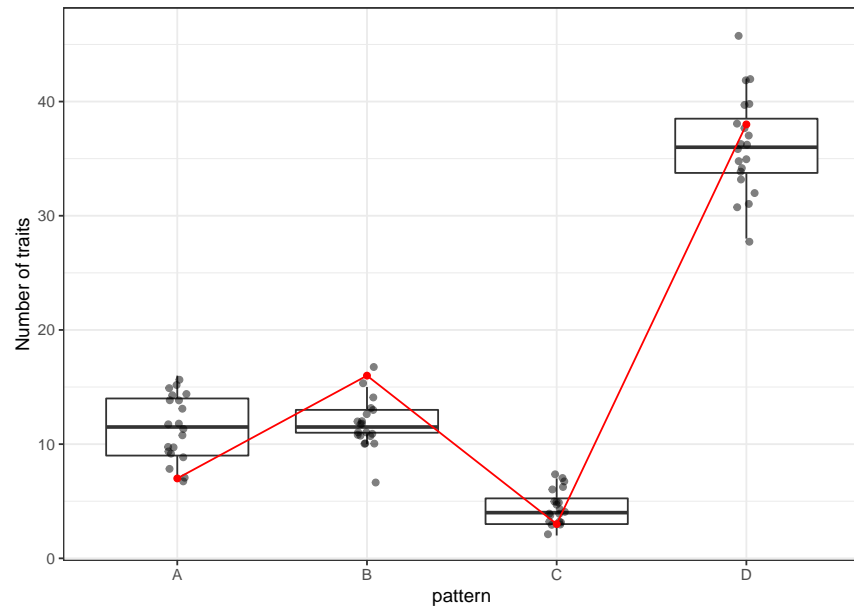


Fig. 3. Number of behaviours for each of the four patterns (*A*, *B*, *C*, *D*) for the parameters $\alpha_e = 0.8$; $\alpha_g = 0.2$, $S = 1$. The red values are the values described for real chimpanzees populations. $N = 20$ runs.

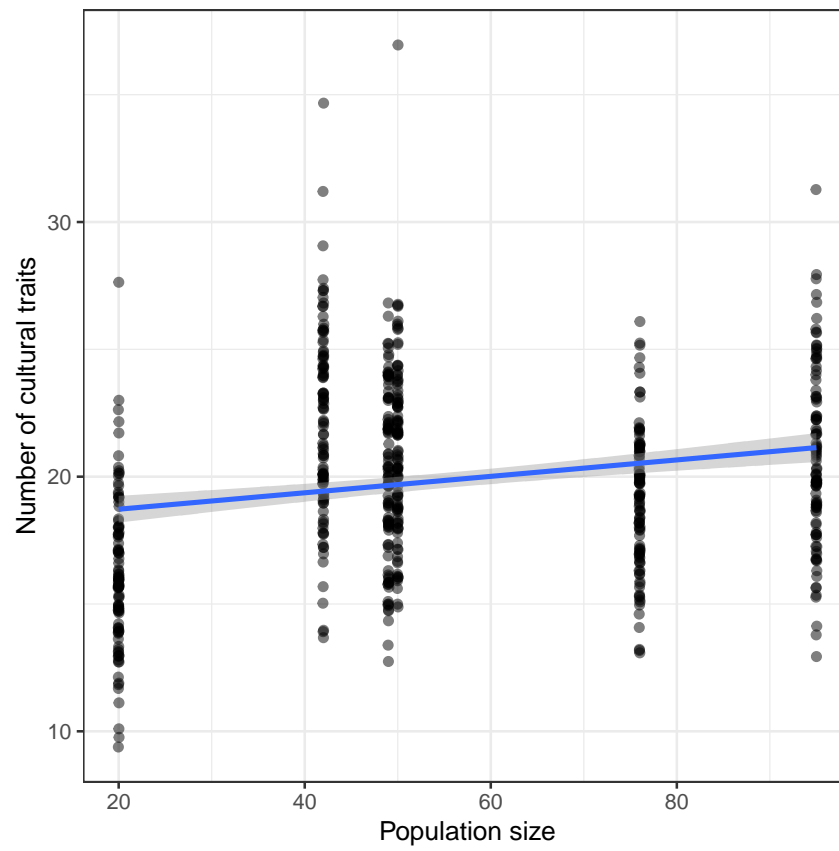


Fig. 4. Number of cultural behaviours for each population ^{various} sizes for the parameters $\alpha_e = 0.8$; $\alpha_g = 0.2$, $S = 1$. The blue line is a linear fit of the data. $N = 100$ runs.