

Culture in oranzees

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cultural transmission | cultural evolution | cumulative culture | chimpanzees culture | individual-based models | animal culture

Cumulative culture, the transmission and improvement of knowledge, technologies, and beliefs from individual to individual, and from generation to generation, is key to explain the extraordinary ecological success of our species (1, 2). Which cognitive abilities underpin human's cumulative 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 at least use social cues to modify their behaviour. Various primates have been shown to possess complex traditions that are socially influenced (3–5). Differently from other primate species, however, humans have 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 (more effective cultural traits at time t than at time $t-1$), and ratcheting (the innovation of cultural traits at time t depends on the presence of other traits at time $t-1$) (7).

Not all human culture needs to be supported by faithful copying (8), but our cumulative culture depends on an ability to transmit and preserve accurately new information. Experiments have indeed shown that humans are capable of copying, and that they routinely copy cross-culturally. More controversial is the claim that other species copy. Claims regarding the existence of non-human great ape cultures based on copying raise a puzzling question: if other species can and do copy, why do they not develop cumulative cultures? There are only two possible answers to this question. Either they do not copy, or copying does not automatically lead to cumulative culture.

Ape primatologists have claimed the existence of copying-based cultures from analyses of observations of wild populations. For example, we examined the population-level distribution of behavioral traits in populations of chimpanzees across seven sites, and argued that this distribution indicated the existence of copying-based cultures in these populations. We developed an individual-based model to assess whether these patterns actually warrant to pinpoint copying as the underlying learning mechanism. We reproduced 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 absence of any copying. While our simulated species, oranzees, can be influenced by social cues (widespread in the animal kingdom, and certainly

present in all apes), we explicitly did not model any copying.

Our results show that, under realistic values of the main parameters, we can reproduce the distribution of behavioral traits found in (3), without any copying required. 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 must have taken place.

Materials and methods

We built an individual-based model that reproduces a world inhabited by six populations of “oranzees”, a hypothetical ape species. The model is space-explicit: the oranzees populations are located at relative positions analogous to the six chimpanzees sites in (3). This is important to determine the potential genetic predispositions and ecological availabilities associated to their possible behaviours (see below). Population sizes are also taken from the sites in (3). Following (10), 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 oranze 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 oranze dies it is replaced by a newborn.

A newborn oranze does not show any behaviour. Behaviours can be innovated at each time step. The process of innovation is influenced by: (i) the oranzees 'state', which depends on the behaviours an individual already possesses, (ii) the frequency of the behaviours already present in the population (“socially-mediated reinnovation” in (12)), and (iii) the genetic propensity and ecological availability locally associated to the behaviour. At the beginning of the simulations, the populations are randomly initialised with individuals between 0 and 25 years old.

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.

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State. In the oranzees world, 64 behaviours are possible. Behaviours are divided into two categories, namely 32 social and 32 food-related behaviours. These figures were chosen to resemble the behavioural categories considered in (3).

In the case of social behaviours, we assume four sub-categories (e.g. 'play', 'groom', etc.) 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 behaviours, 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 into sub-categories, with the differences, with respect to social behaviours, 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 . Here individuals need to balance their nutritional intake, so that their optimal diet consists in a roughly equal number of food for one and the other nutrient. The state, for food-related behaviours, depends on the total amount of food ingested and on the balance between nutrients, and it is calculated as the sum of each sub-category fulfilled (above, for this to happen there needs to be at least one behaviour present) 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 reinnovation. 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 depends 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 reinnovation is socially-mediated (12). When a reinnovation 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 reinnovated.

When the reinnovation 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 then innovated or not 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 for 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 whether is different. If the probability is equal, p_g is randomly drawn. If it is different, we assign the propensity 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 no genetic influences on the behaviour, but that there are no differences between the populations with regard to this aspect.

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 simulations for $t_{\text{max}} = 6000$ (corresponding to 500 years of oranzee-time). For each simulation, following (3), 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 not observed even once in the population.
- *ecological explanations*: a behaviour that is absent because of complete lacking of local ecological availability (i.e., in our model, associated to $p_e = 0$).

Notice the last category in (3) (*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, because we have full knowledge of the output of the simulations.

Finally, to test how well our model compares to the results in wild apes, we calculate the same "patterns" described in (3):

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

Results

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, reinnovation is socially-mediated ($S = 1$). The results show that various combinations of parameters produces a number of cultural behaviours (pattern D) consistent with the 38 found in (3), in absence of any explicit copying mechanism implemented (see Figure 1).

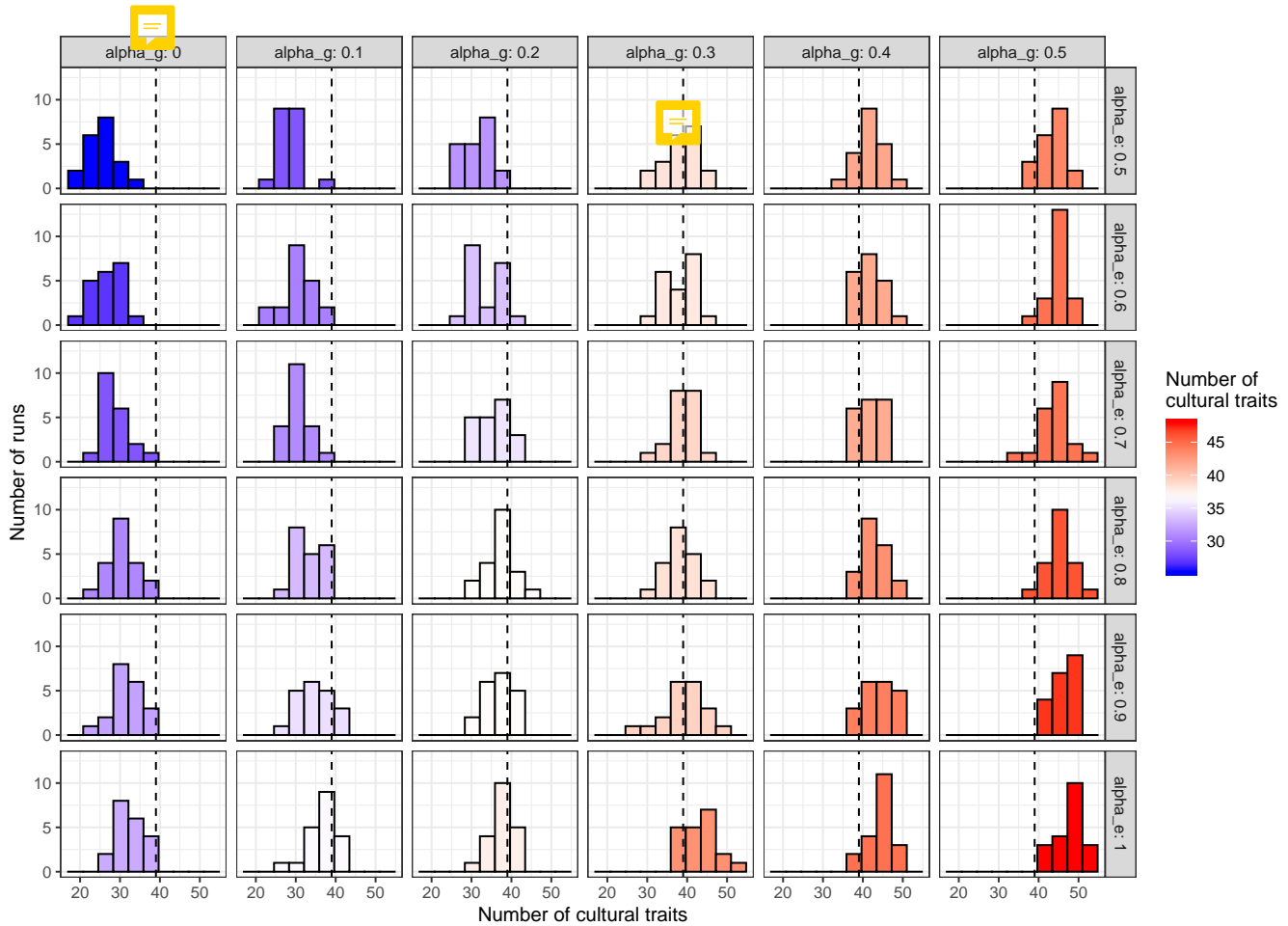


Fig. 1. Number of cultural traits in oranzees, when varying ecological and genetic diversity. Red colour indicates simulation runs that produced more than 38 cultural behaviours; blue colour indicates simulation runs that produces less than 38 cultural behaviours. For all simulations, $S = 1$, α_e and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

We also analyse the effect of the parameter S (proportion of socially-mediated reinnovations), 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 produced less than 38 cultural behaviours), (b) good match with (3), 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 (3), when not all reinnovations are socially mediated.

Our results show that our model not only reproduces very well the number of cultural behaviours (pattern D), but also the number of behaviours classified in the other three patterns (A, B, C) in (3). Figure 3 shows 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 (3) ($\alpha_e = 0.8$; $\alpha_g = 0.2$, $S = 1$). 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 ($p < 0.00001$, $\rho = 0.2$, $N = 600$). In other words, our model reproduces the effect of cultural accumulation relative to population size possibly found in real populations (compare (9, 13, 14)).

Discussion

We developed an individual-based model to examine under which conditions a distribution of behavioral traits analogous to the distribution reported in (3) in chimpanzees could emerge, **crucially**, without allowing for the existence of any copying mechanism. We implemented several details of the original study, including realistic demographic and spatial features, as well as effects of genetic propensity and ecological availability on the behaviours. We also included socially-mediated reinnovation, where social learning merely catalyses individual reinnovation (12).

Our main result is that we can reproduce the wild ape pattern under realistic values of the parameters of genetic propensity and ecological availability, namely null to medium importance of genetic variation, and medium to high importance of ecological variation. While we cannot precisely pin-

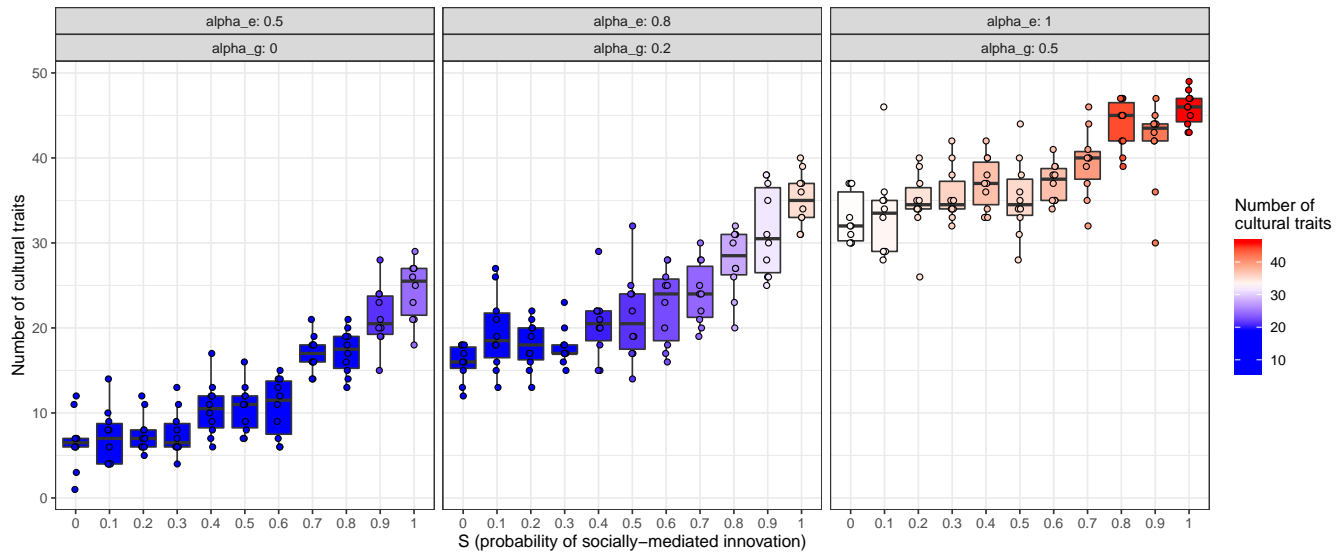


Fig. 2. Cultural traits in oranzees, varying the probability of socially-mediated innovations. Red colour indicates simulation runs that produced more than 38 cultural behaviours; blue colour indicates simulation runs that produces less than 38 cultural behaviours. S , α_e and $\alpha_g = 0$ as indicated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

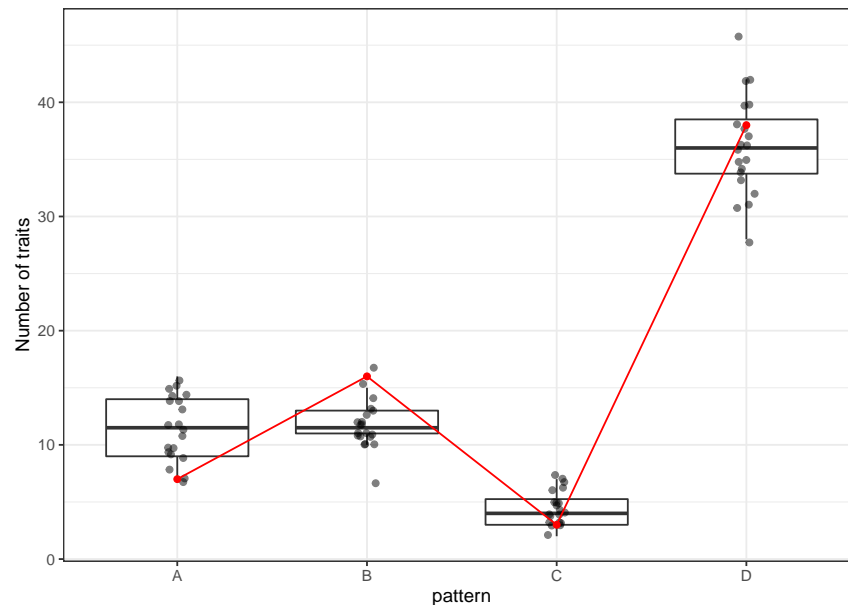


Fig. 3. Number of behaviours for each of the four patterns (*A*, *B*, *C*, *D*) for the parameters $\alpha_e = 0.8$; $\alpha_g = 0.2$, $S = 1$. The red values are the values described for real chimpanzees populations. $N = 20$ runs.

point the exact values that these parameters should have to reproduce real population of chimpanzees (or other apes), we are confident that the range of values explored, and the relative ease by which patterns of cultural behaviours similar to (3) can be produced in the model, strongly suggest that copying is not required for those patterns to emerge. Therefore, ape-like cultural patterns do not ~~and cannot~~ pinpoint copying abilities or necessities. In addition, and as further support to our results, our model not only reproduces the cultural behaviours pattern, but also the proportions among the other patterns, i.e. absent behaviours, behaviours not achieving habitual frequencies at

any site, and behaviours absent because of ecological factors.

In our model, we focused on the mechanism of socially mediated reinnovation, that is, we assumed that members of our hypothetical species, oranzees, had a probability to reinnovate a specific behaviour stochastically linked to how many other oranzees in the population were already showing this behaviour. While this is a realistic assumption [REF] and reproduces in our model the chimpanzees cultural pattern observed in real life in realistic conditions, our results show that it is not necessary. Given certain combinations of parameters, such as higher genetic and ecological diversities, the

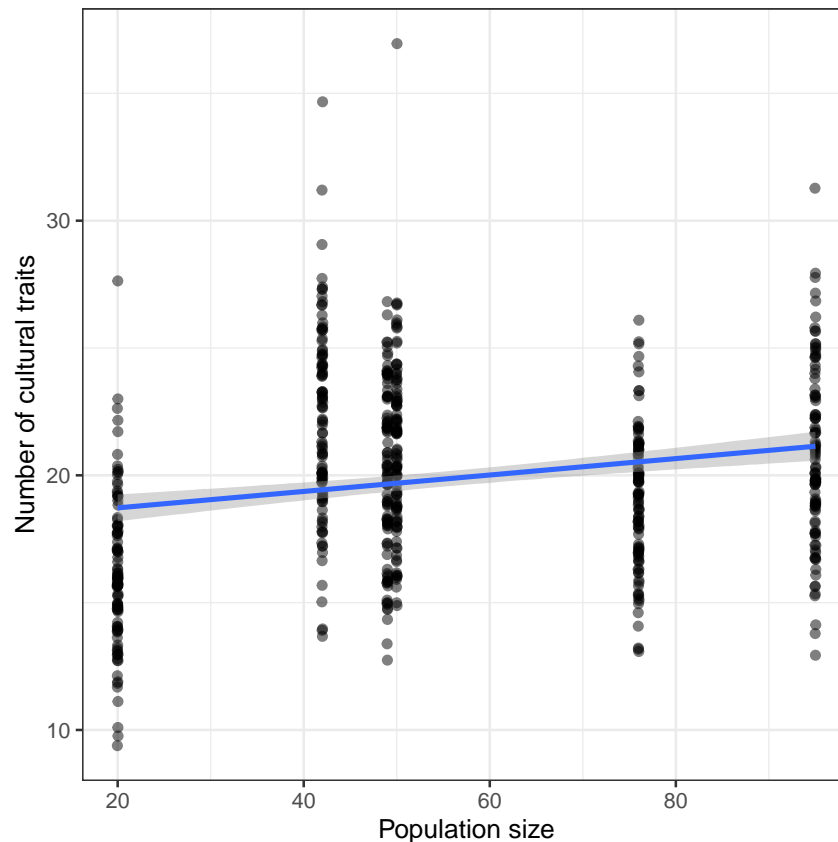


Fig. 4. Number of cultural behaviours for each population for the parameters $\alpha_e = 0.8$; $\alpha_g = 0.2$, $S = 1$. The blue line is a linear fit of the data. $N = 100$ runs.

same cultural pattern can even be obtained when reinnovation is not socially mediated, i.e. if oranzees were not influenced by the behaviours of the other individuals.

Finally, our model reproduces a correlation between population size and number of cultural traits in the six populations. The magnitude of the effect is small, which is to be expected, given that the presence of this correlation in real populations of apes is currently somehow debated. Again, and importantly, this correlation is brought about without copying, so that there is no need to invoke specific “cultural” reasons (e.g. (15)) to explain such pattern here.

More generally, the results of our models suggest caution when deriving individual-level mechanisms from population-

level patterns (see also (16, 17)). Cultural systems, as many others, often exhibit equifinality: the same global state can be produced by different local processes. Models and experiments are crucial to test the plausibility of inferences going from global to local properties.

In conclusion, our model strongly suggest that the data available on the behavioural distributions of chimpanzees populations can not demonstrate that chimpanzees possess cultures influenced by copying, let alone *requiring* copying. This, in turn, may provide the explanation of why their cultures are not cumulative.

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