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Culture in oranzees

Alberto Acerbia, William Snyder, and Claudio Tennie

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

This manuscript was compiled on December 2, 2019 can you pls draft an abstract?

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.

cultural transmission | cultural evolution | cumulative culture | chimpenzees culture | individual based models / animal culture

Cumulative culture, the transmission and improvement 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, 2). Which cognitive abilities underpin humans cumulative cultural capacities, and how these abilities affect the evolution of culture itself are among the most pressing question of evolutionary

Many other species, besides humans, are able to use social cues to modify their behaviour. Various primates have shown to posses complex traditions that are socially transmitted (3– transmitted5). 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 (Colford Galls 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) (7).

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

ApePrimatologists have claimed the existence of copying-based cultures from outcomes of observations of wild populations. (3) examined the population-level distribution of behavioral example* traits in populations of chimpanzees across seven sites, and argued that this distribution proved the existence of different cultures in these populations. We developed an individualbased 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 (as_widespread in the animal kingdom), we did not model any copying.

** ..and certianly present in all apes

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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 orangees 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 orangees populations are located at relative positions analogous to the six chimpanzees sites in (3). This is important to determine the perfect that predispositions and ecological availabilities associated to their possible behaviours (see below). Population sizes are also taken from the sites in (3). 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 tof the simulation represents a month in orangees' life. From when they are 25 years old (t = 300), there is a 1% probability an orangee 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 orangee dies is replaced by a newborn.

A newborn orangee does not show any behaviour. Behaviours can be innovated at each time step. The process of innovation is influenced by: (i) the orangees 'state', which depends on the behaviours an individual already possesses, (ii) the frequency of the behaviours already present in the population ("socially-mediated reinnovation"), 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. XX cite Bandini & Tennie here

State. In the orangees world, 64 behaviours are possible. Behaviours are divided in two categories, namely 32 social and

can you draft one please? 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.

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32 food-related behaviours. These figures where chosen to resemble the behaviours considered in (3).

In the case of social behaviours, we assume four subcategories, 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 orangee has at least one behaviour out of the eight in the sub-category. An orangee 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 $1 - state_{\text{social}}$.

Food-related behaviours are analogously divided in subcategories, 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, here that their optimal diet consist 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 (as 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 $1 - state_{\text{food}}$. (Further details in

Socially-mediated reinnovation. At each time step, all oranzees have a probability of innovation for social and foodrelated behaviours calculated as described above. The specific behaviour an orangee 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. 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 remnovated.

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 beahviours, ecological availability.

Genetic propensity is a probability $p_q(0,1)$, 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. connect paragraphs?

If it 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_q 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 $\alpha_q = 0$ does not mean that there are no genetic influences on the behaviours 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_a , 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 orangee-time). For each simulation, following (3), we classify each behaviour, in each population,

- customary: a behaviour observed in over 50\% of individuals in at least one age class (see SI for how age classes can you send me SI pls? 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 popu-
- concerns ecological explanations is 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 retain complete knowledge.

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

- A: behaviour absent at no site. ape cultural patterns,
- 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 $(\alpha_q = (0, 0.5))$. We run 20 simulations for each combination (for a total of 600 runs). For all, reinnovation is sociallymediated (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).

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,

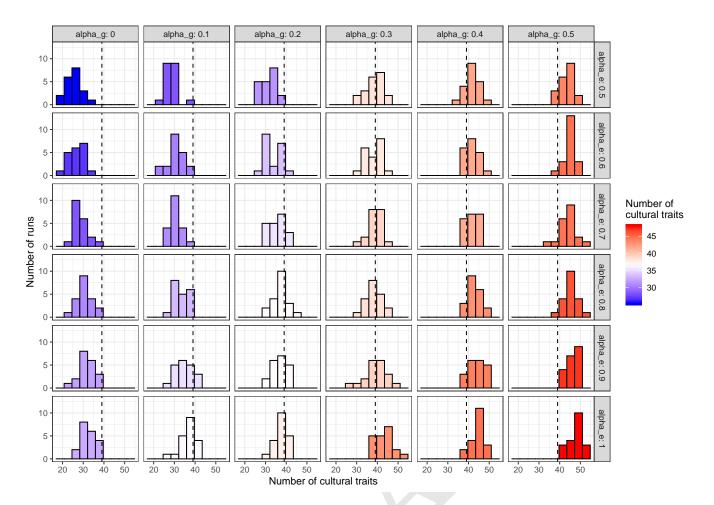


Fig. 1. Number of cultural traits in oranzees, when varying ecological and genetic diversity. Red colour indicates simulation runs that produced more than 38 cultural behaviours; blue colour indicates simulation runs that produces less than 38 cultural behaviours. For all simulations, S=1, α_e and $alpha_g=0$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

where with S=1 simulations produce 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 easily reproduces 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 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 (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 (9, 12, 13).

compare

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 the existence of the condition of the condition with the existence of the condition of the original study, including realistic demographic and spatial features, as well as effects of genetic propensity and ecological availability on the behaviours. Given the widespread availability of non-c. SL, we also

Our main result is that we can reproduce the wine paretern 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 can not precisely pinpoint the exact values that these parameters should have to reproduce real population of chimpanzees, we are confident that the range of values explored, and the relative facility 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. *In addition, and as a further support

we also included SMR (where SL merely catalyses ind. reinnovati on (B&T XX))

*Therefore, ape-like cultural patterns do not and cannot pinpount

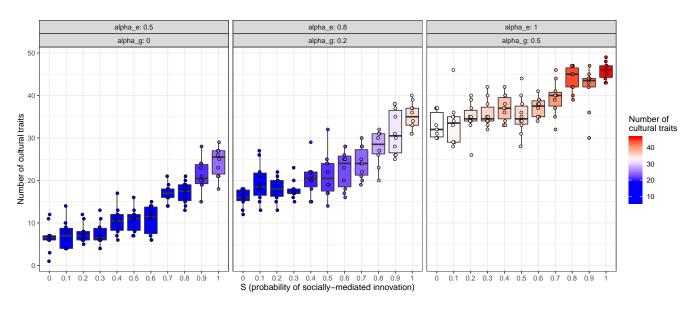


Fig. 2. Cultural traits in oranzees, varying the probability of socially-mediated innovations. Red colour indicates simulation runs that produced more than 38 cultural behaviours; blue colour indicates simulation runs that produces less than 38 cultural behaviours. S, α_c and $alpha_a \equiv 0$ as indicated in the plot. N=10 runs for each parameters combination. --> Into SI. Instead, add here the "WOW WHITEN FIGURE"

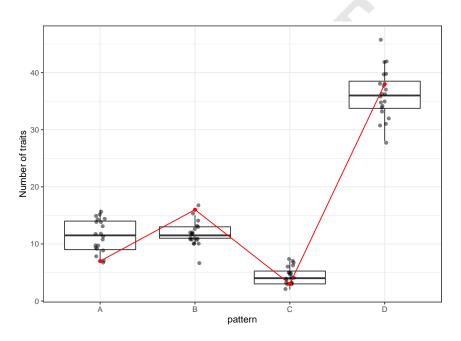


Fig. 3. Number of behaviours for each of the four patterns (*A*, *B*, *C*, *D*) for the parameters $\alpha_e = 0.8$; $\alpha_q = 0.2$, S = 1. The red values are the values described for real chimpanzees populations. $N=20\ \mathrm{runs}.$ This one I would keep in main MS

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, orangees, had a probability to reinnovate a specific behaviour stocastically linked to how many other orangees in the population were already showing this behaviour. While this is a realistic assumption [REF] and

it produces in our model the real chimpanzees cultural pattern observed in realistic conditions, our results show that it is not necessary. IRL Given other combinations of parameters, such as higher genetic and ecological diversities, the cultural patterns can be obtained even when reinnovation is not socially mediated, and of anzees are not influenced by the behaviours of the other individuals.

Werginally, our model reproduces a correlation between population size and number of cultural traits in the six populations. (accumula The magnitude of the effect is small, which is to be expected, tion (XX) given that the presence of this correlation in real populations of apes is somehow debated. Again, and importantly, this

* While this general influence of non-copying social learning mechanisms is covered by the term culture

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it has to be noted that this does not make such culture cumulative (again, the latter likely requires copying social learning mechanisms instead).

** compare Tennie et al. 2010 (floating peanut paper)

***this sentence would need restructuring

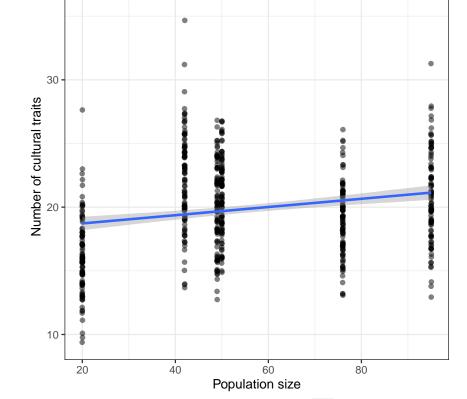


Fig. 4. Number of cultural behaviours for each population for the parameters $\alpha_e=0.8; \alpha_g=0.2, S=1$. The blue line is a linear fit of the data. N=100 runs.

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(as all our results here)

correlation is brought about without copying, so that we do not need to invoke specific "cultural" reasons (e.g. (14)) to explain it:- Such patterns here or elsewhere.

In line with other studies (15, 16), the results of our models suggest caution when deriving individual-level mechanisms from population-level patterns. Cultural systems, as many others, exhibit equinicality: 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. :-) extremely nicely put!!

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 based on copying. This, in turn, may provide the explanation by of why their cultures are not cumulative.

*** let alone requiring copying

ACKNOWLEDGMENTS. ERC, Mima, etc.

* potenially this is a shoot in our foot. here we would need to make clear why only we provide for the 1st time a real answer so, need to say here sth like "other models looking at other factors" or so 1. Henrich J (2015) The Secret of Our Success: How Culture Is doi:10.1371/journal.pone.0009241.

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