Ape cultures do not require behavior copying

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Abstract

While culture is widespread in the animal kingdom, human culture has been claimed to be special due to being cumulative. It is currently debated which cognitive abilities support cumulative culture, but behavior copying is one of the main abilities proposed. One important source of contention is the presence or absence of behavior copying in our closest living relatives, non-human great apes (apes) – especially given that their behavior does not show clear signs of cumulation. Those who claim that apes copy behavior often base this claim on the existence of stable ape cultures in the wild (Whiten et al. 1999; van Schaik et al. 2003). We developed an individual-based model to test whether ape cultural patterns can both emerge and stabilize in the entire absence of any behavior copying, but only allowing for a well-supported alternative social learning mechanism, namely socially-mediated reinnovation, where only the frequency of reinnovation is under social influence, but the form of the behavior is not. Our model reflects wild ape life conditions, including physiological and behavioral individual needs, demographic and spatial features, and the possible range of genetic and ecological variations between populations. Our results show that, under a wide range of realistic values of all model parameters, we fully reproduce the most defining features of wild ape cultural patterns (Whiten et al. 1999; van Schaik et al. 2003). Overall, our results show that ape cultures can both emerge and stabilize without behavior copying. Ape cultures are therefore unable to pinpoint behavior copying abilities, lending support to the notion that behavior copying is, among apes, unique in the human lineage.

Highlights

Human culture is cumulative: it grows in complexity and efficiency, drawing on innovations of previous generations. In contrast, ape cultures are not clearly cumulative. It has been proposed that cumulative culture depends on our ability to accurately transmit and preserve information, with behavior copying as a crucial mechanism. At the same time, researchers have claimed that non-human apes can also copy others' behavior. We show, through computer simulations, that patterns used to infer the existence of behavior copying in wild apes – ape cultures – can be reproduced in full, under realistic conditions, without any behavior copying skills necessary. This shows that the assumption that ape cultures are underlain by behavior copying cannot be proven by the mere existence of ape cultures.

Keywords

Cultural transmission; cultural evolution; cumulative culture; non-human great ape culture; individual-based models; behavior copying.

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Introduction

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 (Henrich 2015; Boyd 2017). Which cognitive abilities underpin human's cumulative cultural capacities, and how these abilities affect the evolution of culture itself are among the most pressing questions of evolutionary human science.

Many species are able to at least use social cues to adjust their behavior. Various primates have been shown to posses traditions that are socially influenced in this way (Whiten et al. 1999; Whiten 2000; van Schaik et al. 2003). Humans, in contrast, have cumulative culture. While there are various definitions of cumulative culture (Mesoudi and Thornton 2018), some of its characteristics are broadly accepted. Cumulative culture requires the accumulation of cultural traits (more cultural traits are present at generation *g* than at time *g-1*), their improvement (cultural traits at generation *g* are more effective than at generation *g-1*), and ratcheting (the innovation of cultural traits at generation *g* depends on the presence of other traits at generation *g-1*) (Acerbi 2019).

While not all human culture needs to be supported by faithful copying (Morin 2015), cumulative culture depends on an ability to accurately transmit and preserve new behaviors. Experiments have indeed shown that humans are capable of copying behaviors, and that they routinely do so cross-culturally (Nielsen and Tomaselli 2010; Berl and Hewlett 2015). More controversial is the claim that other primate species copy behaviors. Arguments regarding the existence of non-human great ape cultures based on behavior copying raise a puzzling question: if other ape species can and do copy behaviors, why do they not develop cumulative cultures? There are only two possible answers to this question: either they do not copy behavior, or copying behavior does not automatically lead to cumulative culture.

Primatologists have claimed the existence of ape cultures based on the ability of behavior copying, drawing on observations conducted on wild populations. For example, researchers examined the population-level distribution of behaviors in populations of chimpanzees across seven sites, and argued that the inter-site differences in the frequency of behaviors proved the existence of behavior copying-based cultures in these populations (Whiten et al. 1999). We developed an individual-based model to assess whether these patterns, and similar patterns in orangutans (van Schaik et al. 2003), actually justify the conclusion that behavior copying is the underlying learning mechanism. We reproduced several details of the original study (Whiten et al. 1999), 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 absence of any behavior copying. While our simulated ape species, *oranzees*, can be influenced by social cues (widespread in the animal kingdom, and certainly present in all apes), we explicitly excluded any behavior copying.

Our results show that, under realistic values of the main parameters, we can reproduce the distribution of behavioral traits found in Whiten et al. (1999), without any behavior copying required. In other words, as oranzees can and do show cultural patterns resembling wild ape patterns, this shows that such patterns do not constitute hard evidence that behavior 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 spatially explicit: the oranzees populations are located at relative positions analogous to the six chimpanzees sites in Whiten et al. (1999). This is important to determine the potential genetic predispositions and ecological availabilities associated with their possible behaviors (see below). Population sizes are also taken from the sites in Whiten et al. (1999). Following Lind and Lindenfors (2010), we use data from Wrangham (2000), 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 Hill et al. (2001). 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 it is replaced by a newborn.

A newborn oranzee does not yet show any behavior. Behaviors can be innovated at each time step. The process of innovation is influenced by: (i) the oranzees 'state', which depends on the behaviors an individual already possesses, (ii) the frequency of the behaviors already present in the population ("socially-mediated reinnovation" in Bandini and Tennie (2017)), and (iii) the genetic propensity and ecological availability locally associated with the behavior. At the beginning of the simulations, the populations are randomly initialized with individuals between 0 and 25 years old.

Oranzees' behaviors and state

In the oranzees' world, 64 behaviors are possible (targeting the 65 behaviors coded in Whiten et al. (1999), but making it an even number from modelling convenience). Behaviors are divided into two categories: 32 social and 32 food-related behaviors. These figures where chosen to resemble the behavioral categories considered in Whiten et al. (1999). Behaviors serve oranzees to fulfill various goals. Oranzees have a 'state' that is based on how many goals are fulfilled in the two main categories of social and food-related behaviors.

In the case of social behaviors, we assume four sub-categories ('play', 'display', 'groom', 'courtship'; note the names are only evocative), each with eight possible different behaviors that serve the same goal. A goal is considered fulfilled if an oranzee shows at least one behavior out of the eight in the sub-category. Oranzees have a 'state' that is based on how many of the four goals are fulfilled. An oranzee has a state value of 0.25 if, for example, it shows at least one behavior in the category 'play', and none of the others, and a state value of 1 if it shows at least one behavior in each sub-category. p_{social}, the probability to innovate a social behavior, is drawn from a normal distribution with mean equal to $1 - state_{\text{social}}$.

Food-related behaviors are analogously divided into sub-categories. Differently from social behaviors, there is a variable number of behaviors in each sub-category. In addition, sub-categories are associated to two different 'nutrients', Y and Z. Here individuals need to balance their nutritional intake, so that their optimal diet consist in a roughly equal number of food for one and the other nutrient. The state, for food-related behaviors, depends on the total amount of food ingested *and* on the balance between nutrients. The state is calculated as the sum of each sub-category fulfilled (as above, for this to happen there needs to be at least one behavior 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 $1 - state_{\text{food}}$.

Socially-mediated reinnovation

At each time step, all oranzees have a probability of innovation for social and food-related behaviors calculated as described above. The specific behavior an oranzee will innovate depends both on the frequency of the behaviors already present in the population, and on the ecological availability and genetic propensity associated to the behavior. A further parameter of the model, S, controls the probability that each reinnovation is socially-mediated (Bandini and Tennie 2017). When a reinnovation is socially-mediated, the probability of innovating each behavior B_i is weighted by its proportional instances in the population among the behaviors of the same category (social or food-related), so that common behaviors are more likely to be reinnovated.

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

Genetic propensity and ecological availability

The behavior selected in the previous step is then innovated or not according to its genetic propensity and, in case of food-related behaviors, ecological availability.

Genetic propensity is a probability $p_g(0, 1)$, assigned independently for each of the 64 behaviors. A parameter of the model, α_g, determines the probability that the genetic propensity of each behavior 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 farthest site where $p_g = 0$, the associated behavior cannot possibly be expressed (see SI). Notice that $\alpha_g = 0$ does not mean that there are no genetic influences on the behavior, 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 behaviors, 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 $t_{\max} = 6000$ (corresponding to 500 years of oranzee-time). For each simulation, following Whiten et al. (1999), we classify each behavior, in each population, as:

- *customary*: a behavior 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 behavior observed in at least two individuals across the population.
- *present*: a behavior observed in at least one individual across the population.

- *absent*: a behavior not observed even once in the population.
- *ecological explanations*: a behavior that is absent due to a complete lack of local ecological availability (i.e., in our model, associated to $p_e = 0$).

Notice that one additional category in Whiten et al. (1999) (*unknown*, i.e. "the behavior has not been recorded, but this may be due to inadequacy of relevant observational opportunities") does not apply in our case, because we have complete knowledge of the output of the simulations.

Finally, to test how well our model compares to wild apes, we calculate the same "patterns" described in Whiten et al. (1999):

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

Further details of the model implementation and of how outputs are processed are available in SI. The full code of the model allowing to reproduce all our results, plus a detailed description of the model development is available in a dedicated GitHub repository, at https://github.com/albertoacerbi/oranzees.

Results

We are particularly interested in the realistic parameter conditions of moderate to high environmental variability (i.e. α_e from 0.5 to 1) and zero to moderate genetic differences (i.e. α_g from 0 to 0.5). We ran 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 produce a number of cultural behaviors (pattern D) consistent with the 38 found in Whiten et al. (1999), in absence of any explicit copying mechanism being implemented (see Figure Figure 1). In Figure Figure 2, we reproduce the output of a run where 38 cultural behaviors were found, and how they were classified in each of the six simulated populations, using a visualization inspired by Whiten et al. (1999).

We also analysed the effect of the parameter S (proportion of socially-mediated reinnovations), in three conditions (see Figure S4): (a) no genetic differences and intermediate ecological differences (compare to the high-left corner of Figure Figure 1, where with $S = 1$ simulations produce less than 38 cultural behaviors), (b) one of the conditions that produce good match with Whiten et al. (1999), namely $\alpha_e = 0.8$ and $\alpha_g = 0.2$, and (c) intermediate genetic differences and high ecological differences (compare to the low-right corner of Figure Figure 1, where with $S = 1$ simulations produce more than 38 cultural behaviors). As expected, decreasing S decreases the number of cultural behaviors. Conditions where, with $S = 1$, there were more than 38 cultural behaviors could still produce results analogous to Whiten et al. (1999), given that not all reinnovations are socially mediated.

As a further proof of our model's fit with empirical data, our outputs not only accurately reproduce the number of cultural behaviors (pattern D), but also the number of behaviors classified in the

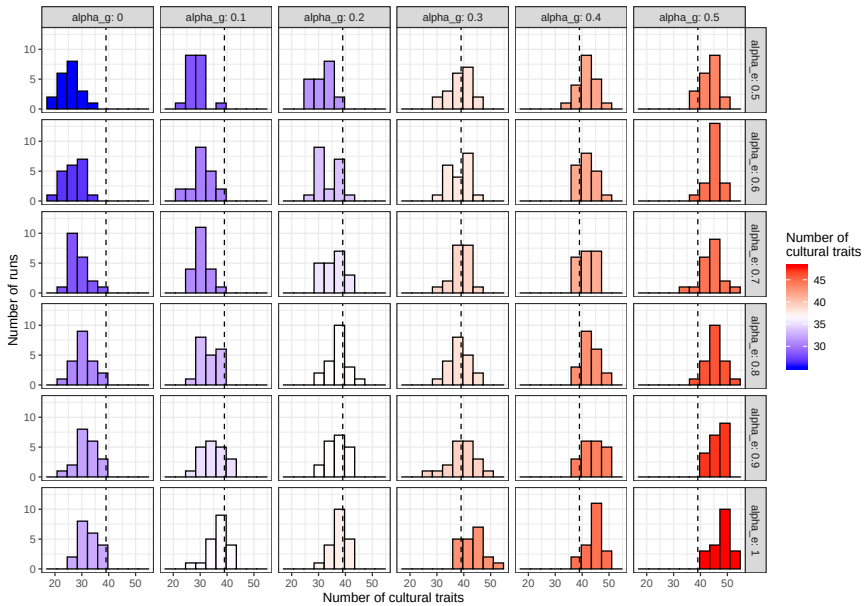

Figure 1: Number of cultural traits in oranzees, when varying ecological and genetic diversity. Red color indicates simulation runs that produced more than 38 cultural traits (the number of cultural traits identified in 1); blue color indicates simulation runs that produced less than 38 cultural traits. For all simulations, $S = 1$, α_e and α_g as indicated in the plot. $N = 20$ runs for each parameters combination.

other three patterns (A, B, C, see above) in Whiten et al. (1999) (see Figure S5).

Finally, we ran 100 simulations for one of the conditions where we have a good match for the number of cultural behaviors in Whiten et al. (1999) ($\alpha_e = 0.8; \alpha_g = 0.2, S = 1$). In each simulation, we recorded, for each population, the number of behaviors (habitual + customary + present) that are also classified as cultural (see Figure S4). 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 an effect of cultural accumulation (i.e. increased number of expressed behaviors) relative to population size possibly found in real populations - see (Whiten and Schaik 2007; Lind and Lindenfors 2010; Kühl et al. 2019) - again, in absence of behavior copying.

Discussion

We developed an individual-based model to examine under which conditions a distribution of cultural traits analogous to the distribution reported in Whiten et al. (1999) in chimpanzees could emerge, crucially, without allowing for the existence of any behavior copying mechanism. We implemented several details of the original wild ape study, including realistic demographic and spatial features, as well as effects of genetic propensity and ecological availability on the behaviors. Given the widespread availability of non-copying variants of social learning across the animal kingdom, we also included socially-mediated reinnovation, where social learning merely catalyzes individual reinnovation, without any behavior copying (Bandini and Tennie 2017).

Our main result is that we can reproduce the general pattern observed in populations of wild apes

Figure 2: Example of a simulation run that produces 38 cultural traits ($S = 1$, $\alpha_e = 0.8$, and $\alpha_g = 0.2$). Color icons indicate customary behaviors; circular icons, habitual; monochrome icons, present; clear, absent; horizontal bar, absent with ecological explanation. The names of the behaviors are only evocative, see SI for a complete list.

under realistic values of the parameters of genetic propensity and ecological availability, namely zero to medium importance of genetic variation, and medium to high importance of ecological variation. Our model cannot precisely determine which exact values of these parameters produce the patterns in real populations of chimpanzees (or other apes). However, we are confident that the range of values we explored, and the ease by which patterns of cultural behaviors similar to Whiten et al. (1999) can be produced, strongly suggest that behavior copying is not required for such patterns to emerge. Therefore, ape-like cultural patterns (Whiten et al. 1999; van Schaik et al. 2003) do not and cannot pinpoint behavior copying abilities. In addition, and as further support to our results, our model not only reproduces the cultural behavioral patterns, but also the proportions among the other observed patterns, i.e. absent behaviors, behaviors not achieving habitual frequencies at any site, and behaviors 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 behavior stochastically linked to how many other oranzees in the population were already showing this behavior. While this is a realistic assumption (Tennie, Call, and Tomasello 2010) and while it reproduces in our model the chimpanzees' cultural pattern observed in realistic conditions, our results demonstrate that it is not always necessary. Given certain combinations of parameters, such as higher genetic and ecological diversities, the same population level pattern can be obtained even when reinnovation is not socially mediated, i.e if oranzees are not influenced by the behaviors of the other individuals in their populations. That is, similar patterns can exist when the underpinning individual-level mechanisms are not cultural even in a minimal way (Neadle, Allritz, and Tennie 2017). However, socially mediated reinnovation is likely required to explain observed differences in behavioral frequencies between the subset of ape populations that exist in genetic contact and that share similar environments (Langergraber et al. 2011).

Finally, our model reproduces a reported correlation between population size and number of cultural traits in the six populations (Whiten and Schaik 2007; Lind and Lindenfors 2010; Kühl et al. 2019). The magnitude of the effect is small, which is to be expected, given that the presence of this correlation in real populations of (human and non-human) apes is currently debated (Vaesen et al. 2016). Notice that this correlation is brought about without any behavior copying, so that there is no need to invoke reasons concerning details of cultural transmssion (e.g. Henrich (2004)) to explain such a pattern.

More generally, the results of our models suggest caution when deriving individual-level mechanisms from population-level patterns (see also (Acerbi et al. 2016; Barrett 2019)). Cultural systems, as many others, 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 suggests that the data available on the behavioral distributions of apes populations cannot demonstrate that ape possess cultures influenced by behavior copying, let alone *requiring* behavior copying. This, in turn, may provide an explanation to why ape cultures are not cumulative: as cumulative culture requires at minimum behavior copying, we should not expect any species lacking this mechanism to develop it.

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Supplementary Information for *Ape cultures do not require behavior copying*

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Additional model information

This document provides additional information on the individual-based model described in the paper *Ape cultures do not require behavior copying*. The full code to run the model and to reproduce the results can be found in https://github.com/albertoacerbi/oranzees, together with a detailed documentation of the model development.

The oranzees' world

The oranzees model is an individual-based model, fully written in R, that reproduces a world where six populations of "oranzees" (a hypothetical ape species) live. The model is spatially-explicit: the six populations are located at relative positions analogous to the six populations of chimpanzees in Whiten et al. (1999) - see Figure 1. For modelling convenience, we put these locations approximately in the center of a 1000 x 1000 squared environment in order to be able to process their relative distances, that we use to calculate genetic propensity and ecological availability of the behaviors (see below).

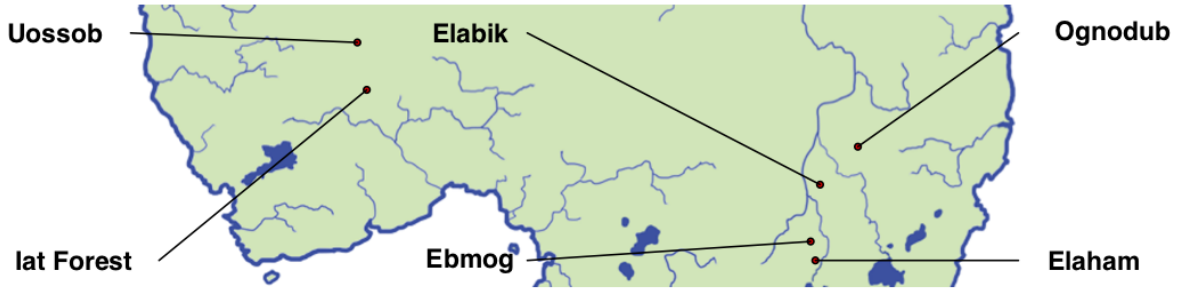

Figure 1: Location of the six populations of oranzees.

The population sizes are also taken from the real chimpanzees populations considered in the study above. Following Lind and Lindenfors (2010), we use data from Wrangham (2000):

Group	Population size
Uossob	20
Elabik	42
Ognodub	49
Iat Forest	76
Ebmog	50
Elaham	95

Geographical gradient for genetic propensity and ecological availability

As described in the main manuscript, two parameters of the models, α_g and α_e, determine the probability that the genetic propensity and ecological availability associated to the behaviors are equal for all the six populations, or if they differ among the populations.

Independently for each behavior, if genetic propensity (or ecological availability) is equal, the probability associated (p_g or p_e) is a randomly drawn number between 0 and 1, the same for all six populations. If they are not equal, the values of p_g (or p_e) are assigned using a geographical gradient, by choosing a random point in the oranzees' world, and calculating its distance to each population. Distances are then transformed to p_g (or p_e) by rescaling them between 0 and 1, so that for the farther population $p_g = 0$ i.e. the associated behavior will be impossible to express (or $p_e = 0$ i.e. the associated behavior will be absent with an "ecological explanation").

In the example in Figure 2, a particular behavior will have $p_g = 1$ (or $p_e = 1$) in the Ognodub site, $p_g = 0$ (or $p_e = 0$) in Iat Forest and Uossob, and intermediate values in the other sites.

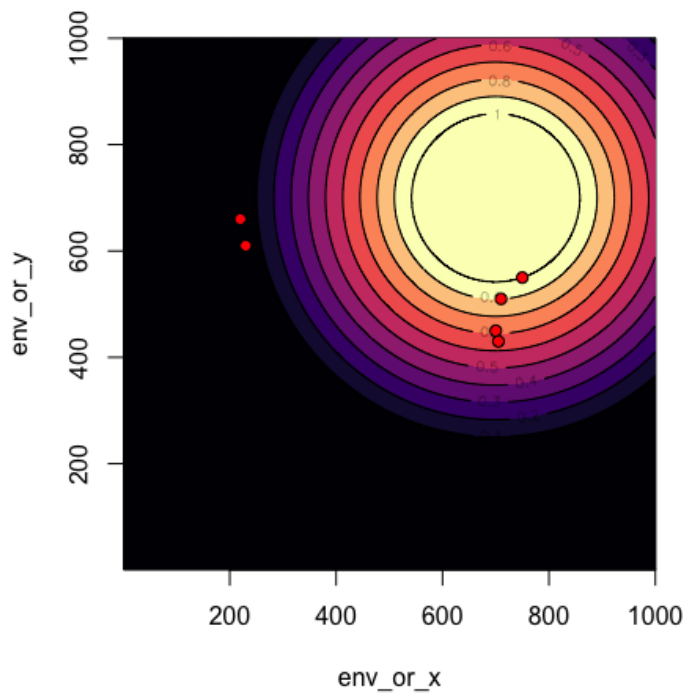

Figure 2: Example of calcualtion of p_g (or p_e). The red points represent the oranzee populations. The color gradient represents the value of p_g (or p_e).

Sub-categories of behaviors

There are 64 behaviors possible in the model (inspired by the 65 coded in Whiten et al. (1999), but made into an even number from modelling convenience), divided in two main categories: "social" and "food-related". Each category is further subdivided in sub-categories. Sub-categories, for food-related behavior, are further assigned to specific "nutrients". This information is used to calculate the oranzee's state according to its behavior (see main manuscript). The names of behaviors and of the sub-categories are only evocative. They are used to illustrate our results in Figure 2 (main manuscript).

Social

Sub-category	Behavior
Play	fruit-missile
Play	slap-fight
Play	air-split
Play	leaf-mask
Play	whistle
Play	pebble-tease
Play	tumbling
Play	brick-fall
Display	stone drop
Display	branch pull-release
Display	arm-cross
Display	two-hand-drum
Display	splash
Display	arm-swing
Display	explode-leaf
Display	contorsionist
Groom	tool back-scratcher
Groom	hand back-scratcher
Groom	tongue-bathe
Groom	tooth-pick
Groom	dirt-shower
Groom	ant-shower
Groom	q-tip
Groom	exfoliate-fruit
Courtship	flower-offer
Courtship	hand-stand
Courtship	rope-swing
Courtship	leaf-fan
Courtship	wreath-clutch
Courtship	ear-pull
Courtship	kissy-hand
Courtship	hop-dance

Food-related

Sub-category	Behavior	Nutrient
Fruit-hammer foraging	wood-wood	Y
Fruit-hammer foraging	wood-stone	Y
Fruit-hammer foraging	stone-wood	Y
Fruit-hammer foraging	stone-stone	Y
Fruit-hammer foraging	bone-wood	Y
Fruit-hammer foraging	bone-stone	Y
Fruit-hammer foraging	wood-ground	Y
Fruit-hammer foraging	stone-ground	Y
Stick-based foraging	stick-throw V	Z
Stick-based foraging	stick-throw A	Z
Stick-based foraging	fish-stab	Z
Stick-based foraging	hedgehog-flick	Z
Stick-based foraging	worm-hook	Z
Stick-based foraging	bird-probe	Z
Stick-based foraging	fish-hammer	Z
Stick-based foraging	spin-seed	Z
Anvil smash	anvil-smash S	Y
Anvil smash	anvil-smash W	Y
Anvil smash	smash-ground	Y
Anvil smash	drop-ground	Y
Rolling pin techniques	rolling-wood	Z
Rolling pin techniques	rolling-stone	Z
Rolling pin techniques	rolling-bone	Z
Rolling pin techniques	rolling-other	Z
Insect swatting	bug-clap	Y
Insect swatting	stick-insect	Y
Fish stunning	fish-stun-stone	Z
Fish stunning	fish-stun-wood	Z
Tortoise-flip	tortoise-drop-on-stone	Y
Potato-mash	tuber-mash	Z
Clubbing	mammal-clubbing	Y
Egg cracking	egg-crack	Z

Example of single run

Figure 3 shows an example of the entire history of all behaviors in a single run, for a single population (geographical location and population size are based on "Uossob"), with $\alpha_g = 0.2$, $\alpha_e = 0.8$, and $S = 1$, i.e. one of the combination of parameters that produces a number of cultural behaviors similar to Whiten et al. (1999).

Figure 3: Example of a single run with $\alpha_g = 0.2$, $\alpha_e = 0.8$, and $S = 1$. The plots show the frequencies of the 64 possible behaviors, divided in panels by sub-category.

Age classes to calculate customary behaviors

To determine *customary* behaviors, we need to define age classes for individuals (the definition of customary behaviors, from Whiten et al. (1999) is a behavior observed in over 50% of individuals in at least one age class). We define three age classes as follows:

- *adults*: individuals that are more than 16 years old.
- *subadults*: individuals between 8 and 16 years old.
- *juveniles*: individuals that are less than 8 years old.

Supplementary figures

Figure S4

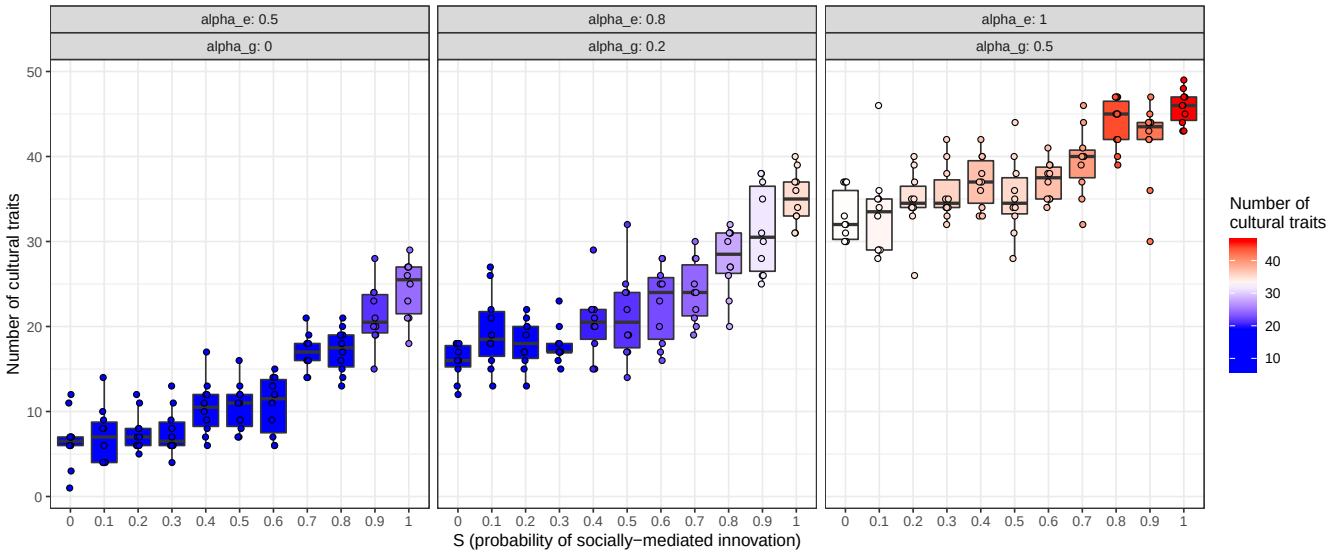

Figure 4: Cultural traits in oranzees, after varying the probability of socially-mediated innovations. Red color indicates simulation runs that produced more than 38 cultural behaviors (the number of cultural traits identified in 2); blue color indicates simulation runs that produces less than 38 cultural behaviors. S, α_e and α_g as indicated in the plot. $N = 10$ runs for each combination of parameters.

Figure S5

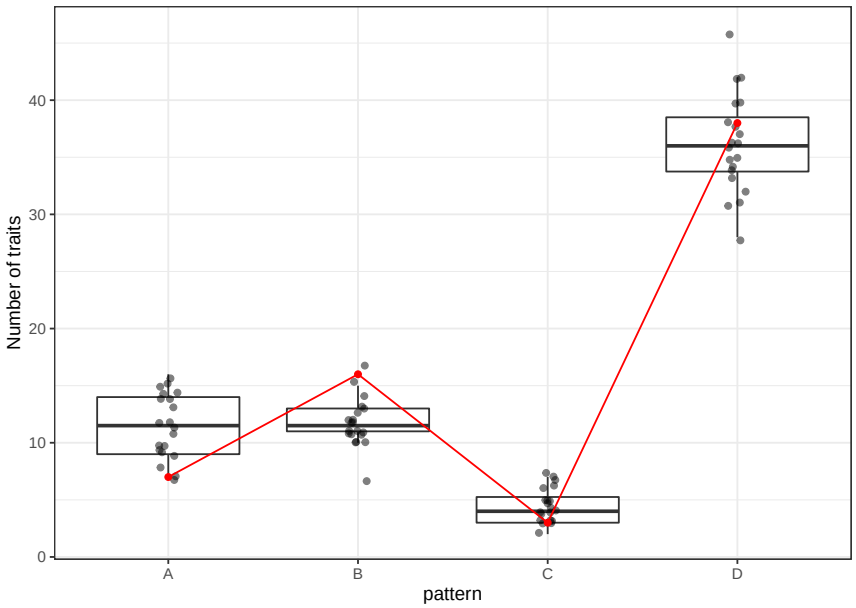

Figure 5: Number of traits for each of the four patterns (*A*, *B*, *C*, *D*, see description in the main manuscript) for the parameters $\alpha_e = 0.8; \alpha_g = 0.2, S = 1$. The red values are the values described for real chimpanzees populations. $N = 20$ runs.

Figure S6

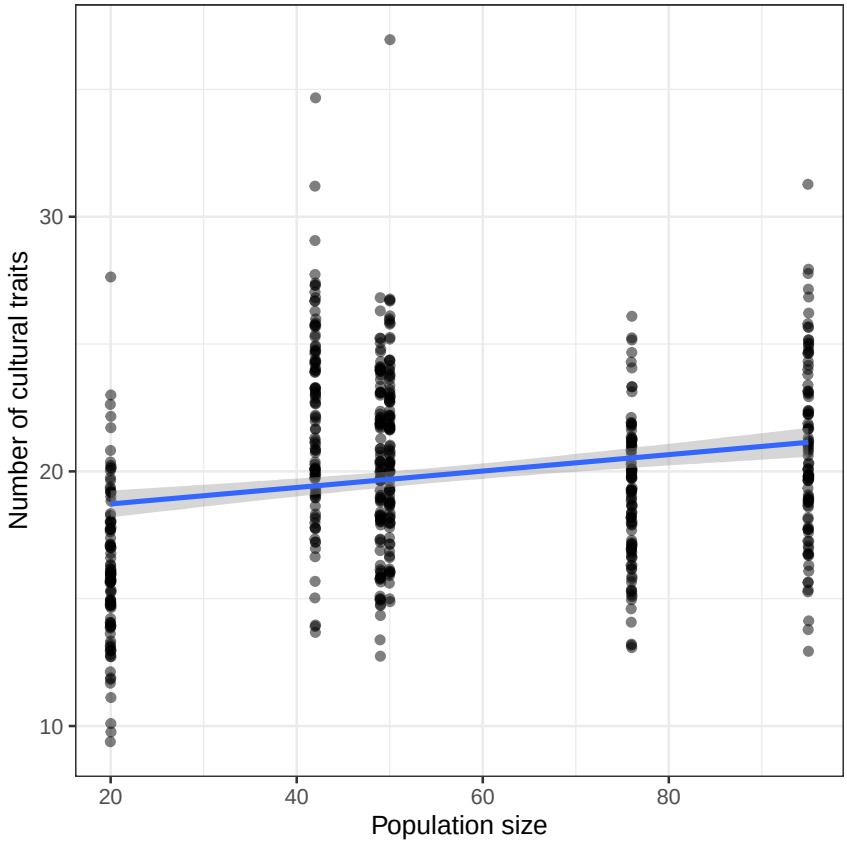

Figure 6: Number of cultural traits for each population for the parameters $\alpha_e = 0.8; \alpha_g = 0.2, S = 1$. The blue line is a linear fit of the data. $N = 100$ runs.

References

Lind, Johan, and Patrik Lindenfors. 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). https://doi.org/10.1371/journal.pone.0009241.

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