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Simulation and social network analysis provide insight into the acquisition of tool behavior in hybrid macaques

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Abstract

The pathways through which primates acquire skills are a central focus of cultural evolution studies. The roles of social and genetic inheritance processes in skill acquisition are often confounded by environmental factors. Hybrid macaques from Koram Island, Thailand provide an opportunity to examine the roles of inheritance and social learning to skill acquisition within a single ecological setting. These hybrids are a cross between tool-using Burmese long-tailed (*Macaca fascicularis aurea*) and non-tool-using common long-tailed macaques (*Macaca fascicularis fascicularis*). This population provides an opportunity to explore the roles of social learning and inheritance processes while being able to exclude underlying ecological factors. Here, we investigate the roles of social learning and inheritance in tool use prevalence within this population using social network analysis and simulation. Agent-based modeling (ABM) is used to generate expectations for how social/asocial learning and inheritance structure the patterning in a social network. The results of the simulation show that various transmission mechanisms can be differentiated based on associations between individuals in a social network. The results provide an investigative framework for discussing tool-use transmission pathways in the Koram social network. By combining ABM, network analysis, and behavioral data from the field we can investigate the roles social learning and inheritance play in tool acquisition of wild primates.

Introduction

The emergence of tool use is argued to have facilitated the adaptive success of the human lineage [1]. Thus, the pathways through which tool use is transmitted across generations are a primary focus of cultural evolution studies [2–4]. While there is a consensus that tool use arises as the result of a combination of genetic and social processes, the contribution of these factors and their evolutionary implications continues to be debated [5–11]. According to the cognitive niche hypothesis tool use arises due to genetic changes that cause an increase in the capacity for problem-solving [9,12]. Selection for these cognitive capacities is then reinforced through the construction of tools that mitigate environmental constraints and increase fitness [10,13]. Others have argued that the selection of specific cognitive traits is not necessary as social learning can facilitate the accumulation of information across generations [11,14]. While this process is particularly potent in humans [14], population-scale cultural processes driven by social learning have also been argued to produce diverse behavioral patterns in primate populations [15–19].

As a result, there has been an increasing focus on identifying the mechanisms that non-human primates use to transfer skills between individuals to determine if some share evolutionary roots with those employed by humans [12,18,20–23]. Extensive work on various primate species, including chimpanzees (*Pan troglodytes*), macaques (*macaca fascicularis*), and capuchins (*Sapajus libidinosus*), indicate that the acquisition and transmission of tool-using behaviors are socially mediated [5,24,25,25–30]. Naive individuals often generate observational opportunities for themselves by maintaining proximity to tool users or showing interest in the residual materials associated with behavior [24,25,31,32]. For example, mothers often provide their offspring with observational learning opportunities critical for the acquisition of skills [31,33–35]. On the other hand, certain genetic predispositions are argued to provide the biological basis necessary for tool use [12,13]. For example, genetic evidence of chimpanzees has shown that general factors that influence the capacity to use tools such as problem-solving, motor skills, and social aptitude are heritable [36,37]. However, whether the presence of a behavioral trait within a population is due to social or genetic factors is often obvious at the species level it is more difficult to discern within an individual species. Within a single primate species, the studies of transmission mechanisms often rely on between-group comparisons where researchers determine the influence of a transmission mechanism by attempting to rule out all other factors. However, between-group comparisons of various primate species are often confounded by the influence of ecology on observed patterns [22,38,39]. Moreover, group comparisons investigating whether behavior variation is due to genes or culture have produced contradictory results even when the same data sets are used [13,20,22]. For example, two studies that examined behavioral variation within *Pan* to determine that between-group behavioral variation was the result of cultural processes while the other suggested that these differences were due to genetics [20,22].

Hybrid populations provide a rare opportunity to investigate the social and/or genetic drivers of behavioral variation in a single ecological setting [40–42]. The long-tailed macaques of Koram Island, Thailand are a cross between, the tool using Burmese (*Macaca fascicularis aurea*) and non-tool using common (*Macaca fascicularis fascicularis)* subspecies [13]. The Burmese sub-species habitually use stone tools to forage for marine resources, including crabs, snails, and oysters [43–45]. In contrast, individuals from the common sub-species use tools in neither wild nor captive settings despite prolonged exposure to resources [13,46]. While the Koram population also uses tools to forage for a similar array of marine resources, observations suggest that variation in whether individuals use tools may be linked to differences in genetic contributions from each sub-species [13]. Previous research revealed that only about half of the Koram population were tool users; a substantially lower proportion of tool users than what is observed in a pure Burmese population [13]. A comparison of tool use frequency and phenotype found that individuals who displayed more Burmese-like features (hybrid-like) were significantly more likely to be tool users than those who displayed common-like phenotypes (see [13] for how the phenotype is determined). This work has led to the suggestion that traits conducive to acquiring tool use might be genetically inherited [13].

Observational studies have also provided evidence for socially mediated learning of tool skills [32,34]. Tool use emerges in the Koram individuals after a 3-year associative process [32]. A few months after birth, individuals will begin engaging with tool materials [32]. Over the following 2 years, initial object manipulation gives way to combining objects associated with tool use and eventually using them in percussive actions. Individuals continue to improve in skill and efficiency as they increase in age [32]. Analysis of grooming patterns suggests younger individuals will preferentially associate with older, more skilled tool users throughout this developmental period, further suggesting that social learning may play a role in the acquisition of tool use [34]. These macaques, therefore, provide the rare – potentially only – opportunity to study the social and inherited determinants of tool use within a single wild population of primates.

Social network analysis allows us to characterize and quantify the associative relationships between individuals necessary for understanding information transmission patterns [47–49]. Such studies have successfully combined data regarding associative relationships with the appearance of behaviors in individuals to infer the information transmission mechanism influencing a population [28,29,50–52] For example, network-based diffusion analyses combine social network analysis with data regarding the time and order of when specific individuals first exhibit a behavior within a population [51,52]. Despite the utility of SNA, the application of such analyses to wild primate populations requires multi-generational data that can take years if not decades to amass [53]. In many cases, observational data of primate behavior comprises only one or two generations of associations between individuals and thus lack the longitudinal depth required for network-based diffusion analysis. Therefore, methods that allow researchers to investigate information transmission processes in short-term datasets are needed. In order to develop such methods, however, it is critical to understand how various information transmission mechanisms influence the associations between knowledgeable and naïve individuals within a social network,

Agent-based modeling (ABM) provides an investigative framework through which various processes can be simulated and their influence on social network patterns can be explored. The generative nature of ABM allows us to translate the dynamics associated with various mechanisms of information transfer into datasets that can be analyzed in the same way that real-world data is investigated. Therefore, the outcomes of the ABM can be used to develop tangible expectations for how various mechanisms of information transfer can be detected in real-world datasets. While these expectations do not allow us to make explicit inferences, they do provide an informed and investigative framework for discussing the potential roles of various information transmission processes in a living population.

Here, we investigate how inheritance and social transmission processes potentially influence the associations between tool users and non-tool-users within a group of long-tailed hybrid macaques on Koram Island. We develop an agent-based model to explore how genetic inheritance, social transmission, and asocial transmission processes would structure the associations between tool users and non-tool-users within a social network. The social learning conditions of the ABM assume that naive individuals can only acquire tool use when they are in proximity to a tool user. Whereas, under inheritance conditions, tool use could only be gained via transmission from parents to offspring during reproduction. Under asocial conditions tool use is acquired independently. The associations between tool users and non-tool users elucidated by the models provide useful expectations for how various information transmission mechanisms impose patterning on a social network. We then discuss the associations between tool users and non-tool users observed in the hybrid macaque group on Koram Island in light of the outcomes of ABM. The results of this work, thus, provide a context by which to investigate the underlying mechanisms involved in the acquisition of tool use.

Study Population

Koram Island is situated about 1 km off the shore of the Gulf of Thailand within Khao Sam Roi Yot National Park, Thailand. The island possesses about 3.5 km of coastline consisting of rocky shores with small sandy beaches where the macaques engage in tool-assisted foraging of marine invertebrates at low tide (Figure 1). Over 227 days between October 17, 2013, to December 2, 2014, focal data was collected on 69 individuals from a single group. Focal follow data was collected during a daily four-hour window during low tide when marine invertebrates are accessible for foraging. Individuals were continuously sampled in random order at five-minute intervals culminating in a total 499 of hours of observation and 5990 focal scans. Author AT generated lists of individuals in randomized order and focal samples of individuals were conducted according to these lists. All data was recorded by narrating observations into a voice recorder and then transcribing into excel. During each focal, AT recorded data on tool use behavior including when individuals picked up and dropped tools, the starts, and ends of tool-use bouts, the number of strikes and hammering pattern applied, the type of food processed, and whether the bout was successful. AT also recorded social data including when the focal individual entered and exited a 1m radius of other individuals and the identities of these individuals, as well as the starts and ends of grooming bouts and identities of grooming partners. These data enable us to determine tool user status for all mature individuals (n=42) and construct social networks.

Figure 1: Male macaque using a stone hammer to forage on rock oysters (Photo credit: Amanda Tan)

In 2015, AT collected photographic data of the 42 individuals to assess their facial pelage patterns and assign them to a phenotypic category – common-like or hybrid-like [13,43]. Facial pelage has been shown to be an accurate proxy of phenotype as studies across Southeast Asia indicate that features of facial pelage associated with the two sub-species are distinct [54]. Hybrid individuals are recognized by the presence of varying combinations of common and Burmese features [55]. The hybrid phenotype is more similar to the tool-using Burmese long-tail pattern than the common phenotype implying a greater contribution of Burmese ancestry (See Gumert et al. [13], for a detailed description). To determine the phenotypic category, AT collected photos of the front sides of each individual's face, and an independent rater classified them while blind to the individual's tool-use ability.

Analytical Methods

Characterization of associations during foraging

To investigate the role of various transmission mechanisms on tool use acquisition, associative relationships between tool users and non-tool users during foraging bouts were described using social network analysis [47]. Thus, a directed social network was constructed and quantified based on 1-meter proximity associations of Koram individuals during foraging using the igraph package (v1.3.4) in R (v4.1.2), [56,57]. Connections between individuals were weighted by the number of times they were observed within one meter of each other. A directed social network was chosen because each association is comprised of an individual engaging in foraging activity and an individual within a meter of the active individual. Therefore, the assumed transfer of information is from the active individual to the individual within 1 meter.

The position of each individual within the network was characterized by calculating each individual's eigenvector (EV) centrality score [49]. EV-centrality is a commonly used measure to identify individuals who are most connected within a social group [28,48,58]. This measure has been proven to be important regarding social learning as individuals at the center of primate social networks are more knowledgeable and more likely to learn novel behaviors [28,58]. EV-centrality is calculated as the sum of centralities the of an individual's neighbors [49]. Individuals at the center of a given network have more connections with other individuals and thus have higher EV-centrality values. In addition, since social learning requires to repeat encounters with tool users, each individual was also characterized in terms of their connection strength to tool users (strength). Connection strength characterizes how strong an individual's connection is to another individual [59]. Connection strength to tool users was calculated by summing the weight of each connection that an individual has with the tool using individuals.

Generating expectations for information transmission mechanisms

To place the Koram network analysis within a broader interpretive framework we developed three agent-based models (ABMs) to generate expectations for how social, inheritance or asocial learning mechanisms produce measurable patterns within a social network. The ABMs were developed in Python 3.9 using the agent-based modeling python library MESA [60,61]. The full description of the ABM is provided as supplementary material and the code is actively maintained on the author's git-hub page [62].

General Overview of the ABM environment

While the information transmission mechanisms vary between models, the general conditions of each model are the same. Each model is comprised of 100 agents that move through a 20 x 20 grid cell space, in a random fashion. When the model is instantiated 100 agents are randomly distributed onto the grid space. To match the measured attributes, present within the Koram dataset, agents possess the attributes tool-user-status, phenotype, and age. Tool user status corresponds to whether the agent possesses the ability to use tools. Of the initial 100 agents, 99 are classified as non-tool-users. Phenotype is randomly assigned as either "hybrid-like" or "common-like" to reflect the phenotypic categories within the Koram population. Age is initially assigned by randomly drawing a number between 0 and 100. Age does not equate to years but rather the number of time steps an individual has existed in the grid space. We assign a random number to the age of the initial agents in the simulation to prevent mass die-off events during the simulation. The single remaining agent is given tool-user status, the hybrid-like phenotype, and an age of 25 time steps. To consider that, within the Koram population, tool use is acquired as a part of a multi-year developmental process agents with an age of 25 or less cannot acquire the tool-use trait.

During each time step, each agent moves a unit of 1 time step by randomly choosing one of its neighboring grid cells. Then, agents then have the opportunity to acquire tool use according to the conditions of one of three modeled transmission modes (See below). Each simulation runs until 50% of the population gains the tool use skill, the proportion of tool users present within the Koram macaques [13].

Models transmission mechanisms

Social Learning Model

Under conditions of the social learning model, the tool-use trait is only acquired through interactions with agents who already possess the tool-user trait. During each time step agents have a chance to acquire tool-user status if they move into a grid cell occupied by a tool-using agent. The likelihood that an agent becomes a tool user is determined based on the number of previous encounters with tool users. Each time a naïve agent encounters a tool user, the likelihood that they acquire the trait increases by 1%. While 1% appears to be a small increase, this value was chosen given that the Koram Macaques acquire tool use over a 3-year associative process. Therefore, a 1% increase is appropriate given the rate at which the Koram macaques learn tool use in the wild. Thus, as an agent accrues proximity interactions with tool users, the likelihood of skill acquisition increases.

Genetic Inheritance Model

Under conditions of genetic inheritance, the tool-use trait is passed from parent to offspring via reproduction. Therefore, additional parameters governing reproduction, aging, death, and population size are defined. In addition to the general parameters outlined above, the age of agents increases by a unit of 1 during each timestep. The age of the agent corresponds to the number of time steps the agent has existed in the grid space. Then the agent will then determine if it lives or dies. Whether the agent dies is determined by drawing from a binomial distribution with a baseline death probability of .0001. This baseline is further weighted by the age of the agent by adding the agent of the agent divided by .00001. Therefore, the likelihood of death is kept at any given time-step is low. The death probability is kept intentionally low to ensure that agents remain alive long enough to have a chance to reproduce with another agent.

Agents can also reproduce when they share a grid cell with another agent, creating a new agent with an age of 0. Reproductive events occur when two agents share the same grid cell. During which, a new agent (the "offspring") is created at the same location as the parent agents. The offspring's phenotype is inherited from the parents using the following system: if both parents possess the same phenotype (i.e. "hybrid-like" or "common-like"), then the offspring agent will be assigned this phenotype. If the parents' phenotypes differ from each other, then the offspring's phenotype is assigned based on a random choice. To explicitly model the notion that phenotype predicts tool use - as is suggested by Gumert et. al. [13] - the tool use trait is only inherited when the "hybrid-like" phenotype is also inherited.

Finally, to consider the influence between mothers, their offspring, and the acquisition of tool use, newly born agents move depending on their mother's location. As offspring increase in age, the influence of the mother's location on their movement lessens and their movement eventually becomes random (as defined above). Within the simulation, agents preferentially pick the neighboring grid cell that minimizes the distance from their mother. The probability that agents chose this grid cell equal to two times and age of the agent divided by 100. This ensures agents will almost always follow their mother agents when they are very young but less so when they are older.

Asocial Model

Given that the Koram data is comprised of proximity associations during foraging, it is important to rule out the influence of ecological processes on the structure of the social network. For example, locations of tool-required resources could cause tool users to occupy specific locations within the wider foraging landscape. Such a phenomenon could cause non-random associations between tool-users and non-tool-users simply due to a preference for specific locations as opposed to information transmission. Thus, within the asocial model agents are given a five percent chance to independently acquire the tool use trait after every time step. Moreover, to examine the effect of spatial preference, agents with the tool-use trait will preferentially, according to a user-defined probability, move toward the location of "attractors" that are randomly distributed within the grid space. The chance that a tool-using agent will move towards an attractor was set to 25%. Furthermore, the influence of resource attraction on the preferential association of tool users is likely dependent on the number of resources that require tool use to gain access. If the foraging landscape possesses a single location where tool use is required, then we expect a strong association between tool users because they will all gravitate to a single location. However, if resources are abundant and widespread, the effect of resource attraction on the number of associations between tool users might be weak. To examine this relationship, we varied the number of "attractors" present also varied between 1, 10, and 200.

Generative output

At the end of each simulation, a record of proximity associations between agents is outputted. An association is defined as any time two agents share the same grid cell. In addition, agent-specific information including, age, phenotype, and tool-user status is also exported. These data are then analyzed in the same fashion as the observed data, allowing the ABM data to be investigated in the same manner as the data collected from Koram.

Statistical Analysis

To investigate the outcomes of the data generated by the agent-based model with the observed data from Koram Island, we developed a binomial linear model with a logit function to test the effects of phenotype, age, and foraging associations on tool user status. In addition to the data from Koram Island, this statistical model is also applied to data generated from 30 iterations of each condition of the agent-based model. By applying the same statistical model to both data sets we gain insight into how the variables age, phenotype, EV-centrality, and strength influence the tool use status under various conditions of information transfer. In doing so, it becomes possible to assess the roles of social learning, inheritance, and asocial processes in the acquisition of tool use within the Koram macaques. Code, equations, and measures of performance associated with this model are provided as supplementary material and available on the author's git-hub page.

The response variable is defined as tool user status (*T*). To examine the effect of phenotype on tool-user status, phenotype (*P)* was included as a categorical variable. Moreover, to assess the effect of social network position on tool-user status, EV-centrality (C) and Strength (S) were included as continuous variables. Age (A) was also included in the model as a control variable given that tool use is only observed in individuals after 2.5-3.5 years. To do so, age was broken down into the categories developmental age and tool user age and included as interaction with both phenotype, EV-centrality, Strength. We used uninformed regularizing priors to ensure the model did not produce unrealistic outcomes. Priors for age and phenotype were represented by a normal distribution with a mean of 0 and a standard deviation of 1. The prior for centrality is modeled as Log-Normal distribution as previous studies show that increasing centrality increases the likelihood of receiving new information [28]. Similarly, the prior for strength was also included as a Log-Normal distribution as the more The model was fit to each of the simulated conditions of social learning and inheritance as well as the data from Koram Island using the Hamiltonian Monte Carlo engine in Stan v.2.28.1 [63] using the rethinking package in R v4.1.2 [64].

Results

Simulations

Summaries of the marginal distributions of each parameter under each simulated condition are presented in Tables 1 and 2. However, each parameter cannot be directly interpreted as to its importance in determining the likelihood that an individual is a tool used due to the interactions between the variables. Instead, these values should be viewed in combination with the posterior predictions visualized in Figures 1, 2, and 3. A full summary of the diagnostics and visualizations can be found on the author's GitHub page (S1).

As expected, the effect of age is consistent across all information transmission conditions. Recall that the ABM explicitly prevents the agent under the age of 25 from acquiring the tool-use trait. Therefore, the likelihood that an individual is under the minimum age necessary to acquire tool use is zero. For individuals who are of age to learn to use tools, the variables that influence the likelihood of tool user status are dependent on the mode of information transmission. Under conditions of social learning, both strength and centrality are important factors in determining tool-user status. The average tool user possessed greater strength values than non-tool users in 97% of the model iterations. In terms of EV-centrality, the average tool users possessed greater centrality values than non-tool-users in 77% of the iterations. Strength has the strongest positive effect on the likelihood that an agent is a tool user (Figure 2). Individuals that establish stronger connections with tool users are more likely to become tool users than those who do not. Moreover, EV-centrality also has a positive effect on the likelihood that an individual is a tool user. Individuals that hold central positions are those that have established connections with many other individuals and are therefore more likely to have encountered tool users. However, the effect of EV-centrality is substantially milder when compared to strength. On the other hand, Phenotype has no influence on tool-user status under social learning conditions. This is also to be expected, given that agents do not bias in who they affiliate with according to the phenotype variable. There is little difference in the likelihood that an individual is a tool user when the phenotype is considered (Figure 2).

Figure 2*:* Posterior predictive plots illustrating the effect of social network position (EV-centrality and strength on the x-axis) on tool user status according to phenotype (in individuals old enough to be able to use tools) under simulated conditions of social learning and inheritance, alongside the Koram Island macaques. Note that there is a wide range of uncertainty associated with the data from Koram Island. Nevertheless, the social learning simulation falls within the 89% compatibility interval surrounding the observed data from Koram Island. Whereas the inheritance simulation generally falls outside of this compatibility interval.

In contrast to the social learning condition, phenotype has the greatest effect on tool user status under conditions of inheritance. Agents with a “hybrid-like” phenotype have a 60% chance of being a tool user, whereas those with a “common-like” phenotype have zero chance. Again, this is to be expected as tool use can only be inherited from individuals with a “hybrid-like” phenotype. In addition, there is very little difference between the centrality scores of tool users and non-tool-users with the average difference between tool users and non-tool-users being .01. As a result, centrality has a marginal effect on tool user status under conditions of genetic inheritance (Figure 2). This is because pure inheritance decouples the acquisition of the tool-use skill from social encounters with other tool users. Although it is less prominent than what is observed in the social learning model, strength still has a positive effect on tool-user status. This effect is driven by the spatial associations between new offspring agents and tool-using mothers. Given that offspring attempt to minimize the distance from their mothers, offspring that inherit tool-user status will preferentially associate with tool users, thus increasing their connection strength with tool users.

Table 1: Marginal distributions for each Bayesian model associated with the social learning and genetic inheritance ABM conditions and the Koram data

The results of the asocial model indicate that a mere attraction to specific locations can have a strong effect on the relationship between tool users and non-tool-users within a social network (Table 2). When there is a single attractor the asocial model both measures of strength and EV-centrality have a strong positive effect on the likelihood of tool-user status (Figure 3). This is due to the fact that the attraction to a single or few places in the landscape causes tool users to aggregate at the same locations and are, thus, more likely to associate with each other than non-tool-users. However, as the number of preferred locations increases, this effect diminishes as the increasing number of attractors ensures that tool users do not spend all their time in a single part of the grid space. The positive effect of strength and EV-centrality on tool user status is reduced to a marginal influence as the proportion of attractors reaches 50%.

Table 2: Marginal distributions for each Bayesian model associated with the asocial learning ABM conditions.

Observational data of the Koram macaques

When the observed data from Koram is considered, age has a similar effect on the likelihood that an individual is a tool user when compared with all of the model results. Individuals younger than the age at which tool use typically emerges (infants, juveniles), are unlikely to be tool users regardless of their social network position or phenotype (Table 1). This is to be expected given the multi-year process over which tool use emerges [49]. However, the observed data reveals a negative effect on the likelihood that an individual becomes a tool user that is not as severe as the effects reported in the simulated data (Figure 2). This is likely because there is a time window in which tool use emerges within the Koram individuals as opposed to the set age at which tool use appears. Therefore, within the Koram data, a few individuals may acquire tool use at an earlier age.

Figure 3*:* Posterior predictive plots illustrating the effect of social network position (EV-centrality and strength on the x-axis) on tool user status according to phenotype (in individuals old enough to be able to use tools) under model asocial conditions. Note that the pattern associated with the asocial model is heavily influenced by the number of attractors included in the model.

Among individuals of tool-using age, centrality, and strength both have a positive effect on the likelihood that an individual is a tool user (Figure 2, 4). Individuals who hold more central locations and are more strongly connected with other tool users within the social network are, thus, more likely to be tool users than those on the periphery (Figure 4). Phenotype also influences tool user status among the Koram macaques. Individuals with a hybrid-like phenotype are 11% more likely to become tool-users than those possessing a common-like phenotype. However, this is particularly the case when individuals hold more central positions in the social network. The increased positive effect of possessing a hybrid-like phenotype on tool use falls within the 89% compatibility interval associated with the common-like phenotype.

Figure 4: The Koram social network compared to examples of social networks generated by the simulated conditions of social learning and inheritance. The Koram social network is based on 1-meter proximity data

during foraging. That tool-users (displayed in red) hold more central positions than non-tool-users within the Koram network. The insets (A and B) show examples of simulated social networks under different conditions of information transfer. The layout of the social networks is force-directed, nodes that are closer to each other share more connections with each other than those that are farther away. **A. Social Learning Condition:** An example of a simulation where tool use is transmitted through social learning. Note that tool users are more centrally clustered than non-tool users. **B. Genetic Inheritance Condition:** An example of a simulation where tool use is transmitted through inheritance. Note that there is less of a structured relationship between tool users and non-tool-users.

Discussion

Understanding the pathways through which primates acquire tool use is an important facet of cultural evolution research. Yet, inferring the mechanisms by which wild primates acquire skills remains difficult. The integration of agent-based simulation with a Bayesian linear model provides expectations for how social learning, asocial, and genetic inheritance processes can be distinguished using social network data. Under conditions of social learning individuals that hold more central positions within the network and have stronger connections to other tool users are more likely to be tool users themselves. Under conditions of pure genetic inheritance, neither centrality nor strength will have a positive influence on an individual's status as a tool user. If phenotype and the genetic inheritance of tool use are linked, as they are in the ABM, it should be expected that individuals carrying the 'hybrid-like' phenotype will have a positive effect on tool-user status. Our results also show how food resource distribution can produce preferential associations between tool users. Nevertheless, when food resources are abundant, connection strength to tool users and EV-centrality have little effect on the likelihood that an individual becomes a tool user. These results demonstrate that the statistical model we applied is effective in detecting differences in data sets generated by the three model conditions.

When the social network patterning in the Koram population is compared to the ABM results, a number of consistencies and inconsistencies are observed. These similarities and differences provide an interpretative context through which the influence of information transmission processes on skill acquisition, within a living population, can be discussed. When the Koram macaques are considered, the positive effect of EV-centrality and strength on tool-user status is similar to what is predicted by the social learning model. This finding is also consistent with observations of the associative learning process through which tool use emerges within the group [32]. In comparison with the social learning model, however, the observed effect of strength on tool user status is less strong, whereas the effect of EV-centrality is stronger. The positive effects of EV-centrality and strength on tool user status are also consistent with the asocial model, particularly when the number of fixed resources is few. At face value, the similarities with the asocial learning model may suggest that the pattern observed within the Koram population could simply reflect a preference for tool users to occupy specific places during foraging. However, when the abundance resources on of Koram Island is considered, it is clear that this is not the case. The shores on which the Koram macaques forage are rich in marine resources implying that there is an abundance of locations where tools can be used. Moreover, while oysters are sessile upon a fixed substrate (e.g. rocks and boulders), they are distributed continuously along the rocky shore. In addition, many other marine resources (snails, crabs) that the macaques forage on will change location over time. Thus, it is unlikely that the distribution of resources requiring tool use would cause tool users to preferentially associate with one another simply due to the distribution of resources. Therefore, we argue that the positive effects of EV-centrality and Strength are most likely related to social learning processes.

Research by Gumert et al. [13] shows that 76% of hybrid-like phenotypes are tool users whereas 42% of common-like phenotypes are tool users. This may suggest that some prerequisite components needed for tool use are possibly inherited. Our results maintain some level of uncertainty surrounding the effect of the hybrid-like phenotype on tool-user status (Figure 2). Nevertheless, there is reason to suggest that this effect is biologically meaningful. Previous research on Burmese long-tails (*Macaca fascicularis aurea*) shows that almost 90% of individuals within a single population are tool users [13]. These observations show that the higher proportion of tool-users observed in the hybrid-like individuals is more consistent with the proportion of tool-users observed in Burmese populations. Within the broader context of primate behavior, social learning is understood to play a major role in tool use acquisition [65]. Usually, all members of tool-using primate groups are tool-users [15]. Thus, if social learning were entirely responsible for the prevalence of tool use on Koram Island, we would expect there to be a greater proportion of tool users within the population. Instead, only half of the population exhibit the behavior, the majority of those expressing the hybrid phenotype. Inheritance therefore might play a role in providing the necessary conditions required for tool use. Our work suggests that the actual acquisition of the skill however is facilitated through mechanisms of social learning but is not sufficient to explain tool use in the Koram macaques on its own.

Additional support for this notion could be found by examining mother-offspring relationships. Mothers are an important source of observational opportunities for younger individuals. Therefore, under conditions of social learning, the tool-using preferences of offspring should reflect those of their mother. On Koram island, however, where mother-offspring relationships are known for individuals old enough to use tools, there are at least two instances where the tool user status of the mother is not the same in the offspring. In one instance, a tool-using mother raised an individual that did not become a tool-user. In another, it was the other way around. Though these data are limited, they suggest that offspring may not always mirror the behaviors of their mother.

It is most likely that social and inheritance factors both contribute to the acquisition of tool use within this population. It has already been shown that certain motor control and acquisition of socially learned behaviors in primates are highly heritable [36,37,66]. While all behaviors involving tool use are likely mediated by a combination of inherited and social factors [67,68], the hybrid long-tailed macaques of Koram may be a unique case where inheritance still dictates whether an individual can acquire tool use as a skill within one population. While the simulations presented here allow us to generate expectations under conditions of inheritance, the genetic processes that govern inheritance are likely far more complex in the real world. Further genetic studies therefore can help investigate potential predispositions regarding tool use. This information would help to further entangle requirements that are necessary for the acquisition of tool use, contributing to ongoing discussions regarding the evolution of tool use in human and non-human primates [2,9–11,14,46,69]

Within the context of broader evolutionary theory, hypotheses favoring the selection of cognitive traits that facilitate tool use are often pitted against those that favor cultural explanations as competing hypotheses [9,10,70]. The results of our work suggest that both inheritance and social processes play an active role in the prevalence of tool use within long-tailed macaques. This further suggests that social processes and predispositions need not be mutually exclusive. Thus, these hybrid macaques may be a living example of how predispositions mitigate the acquisition of a socially learned behavior. Such learned behaviors in return may result in the selection of cognitive traits or developmental biases that further promote the prevalence of tool use within a population. The combination of applying agent-based modeling and social network analysis to technological primates provides a novel opportunity to investigate the role of these underlying processes on tool-use prevalence.

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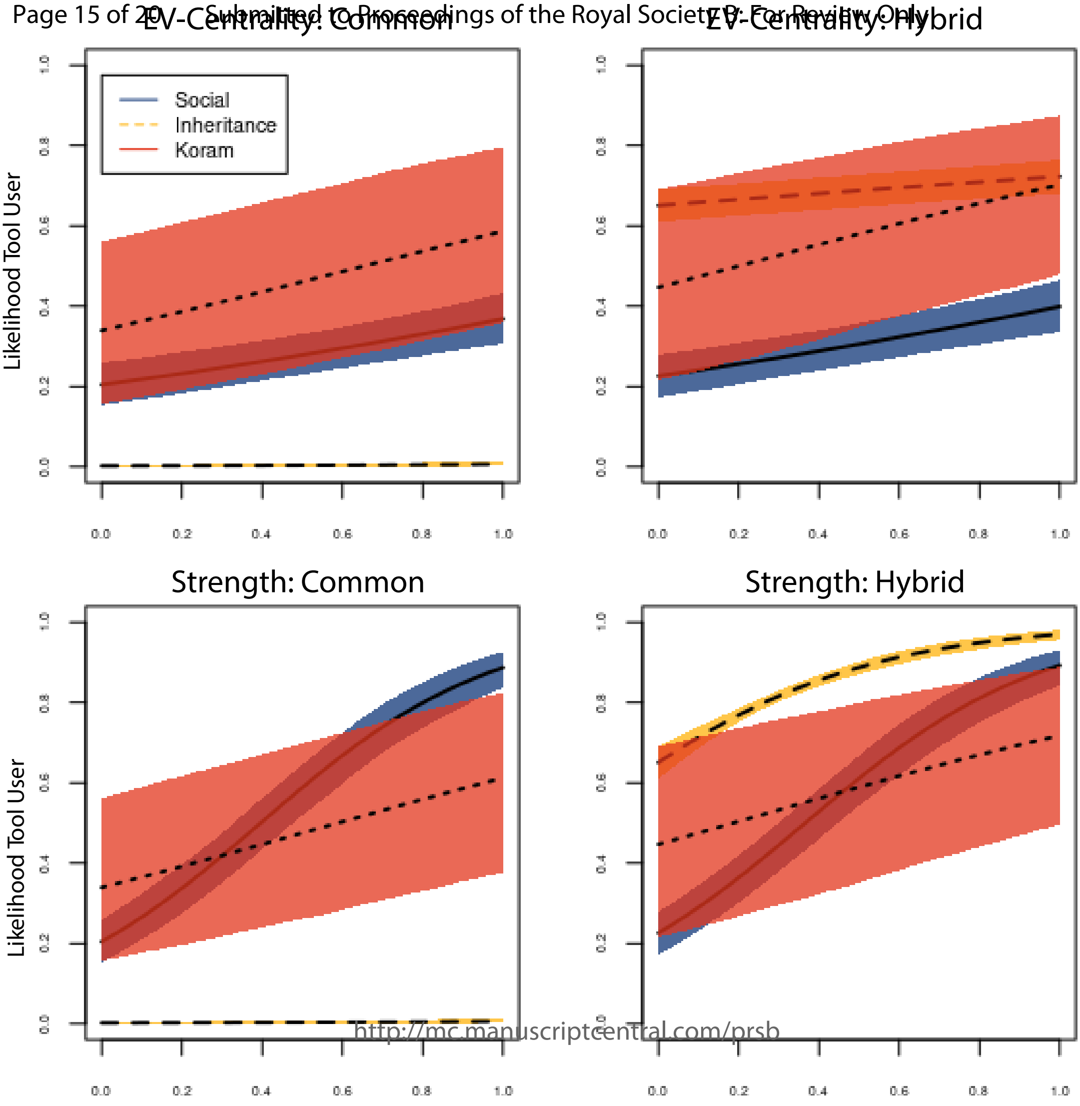
Male macaque using a stone hammer to forage on rock oysters (Photo credit: Amanda Tan)

1244x829mm (72 x 72 DPI)


EV-Centrality: Common
EV-Centrality: Hybrid
Strength: Common
Strength: Hybrid
Social
Inheritance
Koram
Likelihood Tool User
Likelihood Tool User
0.0
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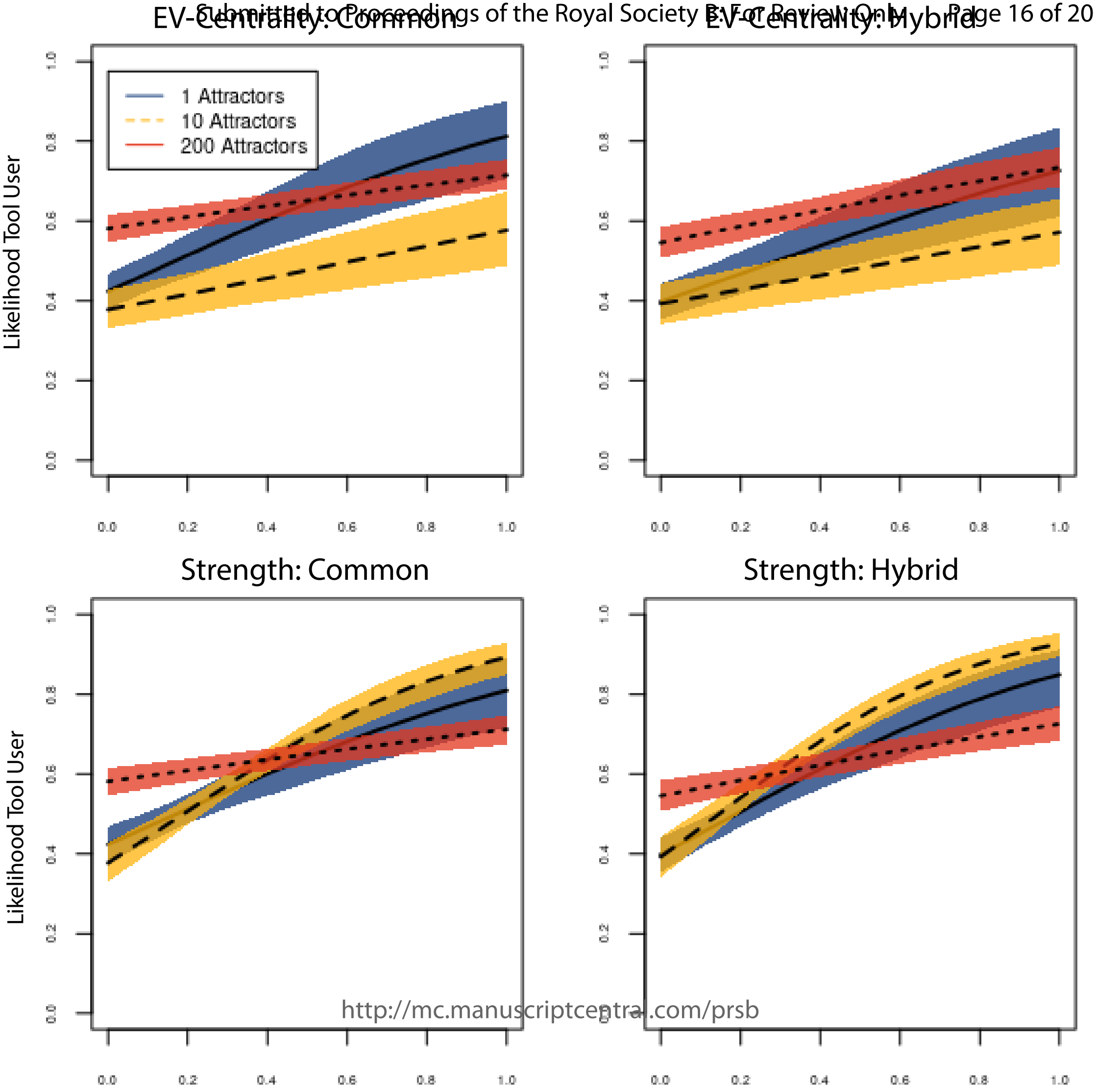
EV-Centrality: Common
EV-Centrality: Hybrid
Strength: Common
Strength: Hybrid
1 Attractors
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Likelihood Tool User
Likelihood Tool User
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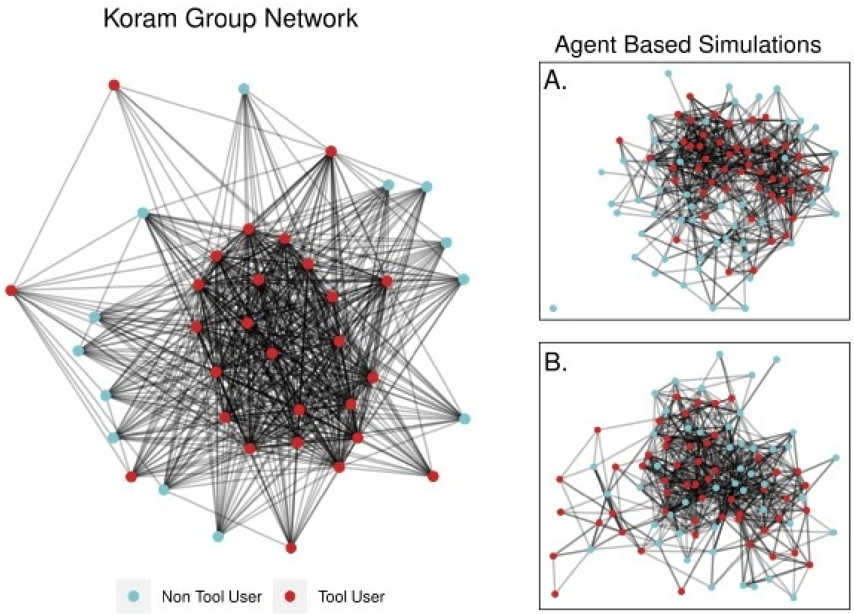
0.8
1.0



The Koram social network compared to examples of social networks generated by the simulated conditions of social learning and inheritance. The Koram social network is based on 1-meter proximity data during foraging. That tool-users (displayed in red) hold more central positions than non-tool-users within the Koram network. The insets (A and B) show examples of simulated social networks under different conditions of information transfer. The layout of the social networks is force-directed, nodes that are closer to each other share more connections with each other than those that are farther away. A. Social Learning Condition: An example of a simulation where tool use is transmitted through social learning. Note that tool users are more centrally clustered than non-tool users. B. Genetic Inheritance Condition: An example of a simulation where tool use is transmitted through inheritance. Note that there is less of a structured relationship between tool users and non-tool-users.

237x169mm (72 x 72 DPI)

Table 1: Marginal distributions for each bayesian model associated with Social Learning and Genetic inheritance ABM conditions and the Koram data

ABM Social Learning

	Mean	Stand Dev	5.50%	94.50%	N effective samples	Rhat4
Intercept (DA, Common Like)	0.002	0.646	0.001	0.005	1157.613	1.000
Intercept (DA, Hybrid)	0.002	0.657	0.001	0.006	1176.759	1.000
Intercept (Adult, Common)	0.203	0.551	0.154	0.259	849.874	1.002
Intercept (Adult, Hybrid	0.224	0.548	0.173	0.279	1039.516	0.999
Centrality (DA, Common)	0.708	0.561	0.634	0.786	1283.313	0.999
Centrality (DA, Hybrid)	0.709	0.561	0.635	0.792	1710.731	0.999
Centrality (Adult, Common)	0.696	0.552	0.629	0.769	889.530	1.001
Centrality (Adult,Hybrid)	0.696	0.551	0.628	0.766	1206.224	0.999
Strength (DA,Common)	0.714	0.565	0.631	0.797	1711.499	0.999
Strength (DA, Hybrid)	0.721	0.569	0.642	0.802	1369.514	1.001
Strength (Adult, Common)	0.969	0.587	0.948	0.982	988.192	1.001
Strength (Adult, Hybrid)	0.967	0.588	0.946	0.981	1091.744	0.993

ABM Genetic Inheritance

	Mean	Stand Dev	5.50%	94.50%	N effective samples	Rhat4
Intercept (DA, Common Like)	0.010	0.662	0.003	0.025	1304.708	0.999
Intercept (DA, Hybrid)	0.004	0.648	0.001	0.009	1469.876	1.000
Intercept (Adult, Common)	0.002	0.649	0.001	0.005	1638.031	0.999
Intercept (Adult, Hybrid)	0.651	0.528	0.613	0.694	887.338	1.001
Centrality (DA, Common)	0.741	0.581	0.651	0.837	1431.673	0.999
Centrality (DA, Hybrid)	0.740	0.580	0.650	0.837	2032.701	0.999
Centrality (Adult, Common)	0.733	0.571	0.650	0.820	1621.914	1.000
Centrality (Adult, Hybrid)	0.584	0.517	0.559	0.612	1499.723	1.000
Strength (DA, Common)	0.736	0.577	0.649	0.828	1486.481	1.000
Strength (DA, Hybrid)	0.738	0.582	0.648	0.835	1184.213	0.999
Strength (Adult, Common)	0.725	0.574	0.640	0.820	1668.426	0.999
Strength (Adult, Hybrid)	0.947	0.586	0.908	0.969	918.716	1.001

Koram Island

	Mean	Stand Dev	5.50%	94.50%	N effective samples	Rhat4
Intercept (DA, Common Like)	0.199	0.751	0.040	0.591	3902.435	1.000
Intercept (DA, Hybrid)	0.082	0.716	0.019	0.260	2965.530	0.999
Intercept (Adult, Common)	0.328	0.647	0.158	0.562	3333.719	1.000
Intercept (Adult, Hybrid)	0.442	0.657	0.215	0.691	2533.928	1.000
Centrality (DA, Common)	0.733	0.576	0.647	0.825	3696.770	1.000
Centrality (DA, Hybrid)	0.731	0.574	0.647	0.823	3720.605	0.999
Centrality (Adult, Common)	0.750	0.581	0.658	0.844	3056.759	0.999
Centrality (Adult, Hybrid)	0.763	0.594	0.662	0.862	2870.686	1.000

Strength (DA, Common)	0.740	0.583	0.647	0.837	3276.850	1.000
Strength (DA, Hybrid)	0.741	0.580	0.651	0.836	3747.252	1.000
Strength (Adult, Common)	0.772	0.597	0.669	0.872	3404.462	1.000
Strength (Adult, Hybrid)	0.778	0.600	0.672	0.880	2524.608	1.002

Table 2: Marginal distributions for each bayesian model associated with the asocial learning ABM conditions

ABM Asocial: Number of Attractors 1, Attractor Strength 25

	Mean	Stand Dev	5.50%	94.50%	N effective samples	Rhat4
Intercept (DA, Common Like)	0.203	0.748	0.042	0.577	1190.877	1.001
Intercept (DA, Hybrid)	0.084	0.715	0.020	0.254	1230.016	0.999
Intercept (Adult, Common)	0.331	0.651	0.154	0.571	1071.159	0.999
Intercept (Adult, Hybrid	0.447	0.655	0.221	0.697	801.963	0.999
Centrality (DA, Common)	0.735	0.575	0.646	0.830	1106.765	1.001
Centrality (DA, Hybrid)	0.731	0.571	0.651	0.822	1017.789	0.999
Centrality (Adult, Common)	0.750	0.586	0.658	0.847	1074.558	0.999
Centrality (Adult,Hybrid)	0.763	0.592	0.661	0.856	826.551	0.999
Strength (DA,Common)	0.737	0.582	0.645	0.834	1062.476	0.999
Strength (DA, Hybrid)	0.744	0.583	0.649	0.838	1147.294	0.999
Strength (Adult, Common)	0.775	0.601	0.668	0.875	981.042	0.999
Strength (Adult, Hybrid)	0.775	0.599	0.669	0.877	908.120	0.999

ABM Asocial: Number of Attractors 10, Attractor Strength 25

	Mean	Stand Dev	5.50%	94.50%	N effective samples	Rhat4
Intercept (DA, Common Like)	0.003	0.664	0.001	0.009	806.218	0.999
Intercept (DA, Hybrid)	0.004	0.657	0.001	0.010	908.367	1.000
Intercept (Adult, Common)	0.417	0.530	0.372	0.464	824.706	0.999
Intercept (Adult, Hybrid)	0.393	0.530	0.349	0.439	807.227	0.999
Centrality (DA, Common)	0.728	0.568	0.648	0.814	1098.770	0.999
Centrality (DA, Hybrid)	0.731	0.573	0.646	0.818	952.881	1.002
Centrality (Adult, Common)	0.857	0.608	0.756	0.926	667.213	0.999
Centrality (Adult, Hybrid)	0.833	0.599	0.732	0.905	670.360	0.999
Strength (DA, Common)	0.724	0.569	0.645	0.811	1180.376	1.000
Strength (DA, Hybrid)	0.729	0.572	0.647	0.818	781.367	0.999
Strength (Adult, Common)	0.874	0.609	0.771	0.933	625.632	0.999
Strength (Adult, Hybrid)	0.917	0.619	0.838	0.960	519.616	1.000

ABM Asocial: Number of Attractors 200, Attractor Strength 25

	Mean	Stand Dev	5.50%	94.50%	N effective samples	Rhat4
Intercept (DA, Common Like)	0.199	0.751	0.040	0.591	3902.435	1.000
Intercept (DA, Hybrid)	0.082	0.716	0.019	0.260	2965.530	0.999
Intercept (Adult, Common)	0.328	0.647	0.158	0.562	3333.719	1.000
Intercept (Adult, Hybrid)	0.442	0.657	0.215	0.691	2533.928	1.000
Centrality (DA, Common)	0.733	0.576	0.647	0.825	3696.770	1.000
Centrality (DA, Hybrid)	0.731	0.574	0.647	0.823	3720.605	0.999
Centrality (Adult, Common)	0.750	0.581	0.658	0.844	3056.759	0.999
Centrality (Adult, Hybrid)	0.763	0.594	0.662	0.862	2870.686	1.000

Strength (DA, Common)	0.740	0.583	0.647	0.837	3276.850	1.000
Strength (DA, Hybrid)	0.741	0.580	0.651	0.836	3747.252	1.000
Strength (Adult, Common)	0.772	0.597	0.669	0.872	3404.462	1.000
Strength (Adult, Hybrid)	0.778	0.600	0.672	0.880	2524.608	1.002