**Supplementary Material 2: Overview, Design Concepts, and Details for the Agent-Based Model presented in “Social learning and predisposition shape tool behavior in hybrid macaques”**

This model description of Reeves\_et\_al\_Macaque\_Social\_Learning (SI1) follows the ODD protocol for agent-based models (Grimm et al., 2010) and is provided as supplementary material to Reeves et al. (In Review). The model was written in Python version 3.8.10 using the Mesa agent-based modeling library (Masad and Kazil, 2015). This code is actively maintained and freely available on the corresponding author’s [GitHub page](https://github.com/reevesj191/Macaque_Tool_Transmission).

**Purpose**

The role that genetic inheritance, asocial, and social processes play in the proliferation of specific behaviors is openly debated. This is because discerning between these processes, let alone observing within a single population remains difficult. While quantitative methods such as social network analysis enable researchers to investigate the pathways through which information is acquired by specific individuals, there are few expectations for how various information transmission mechanisms influence the relationship between naive and knowledgeable individuals within a social network. The purpose of this agent-based model is to generate expectations for how social, asocial, and genetic inheritance information transmission processes structure the relationship between naive and knowledgeable individuals across a social network. These expectations provide an interpretive framework with which the social networks of animal groups can be assessed. With this goal in mind, the model is further tailored to the foraging dynamics of the hybrid long-tailed Macaques from Koram island to aid in inferring the transmission processes associated with the acquisition of tool use. To do so, this model simulates the spread of the “tool user” skill from a single individual to other individuals through two discreet modes of transmission: social, genetic inheritance, and asocial. ***Under conditions of social learning***, a naive individual can acquire the “tool use” skill when they occupy the same grid cell as a knowledgeable individual (henceforth referred to as tool-users). The chance that the naive individual acquires the skill is dependent on the number of previous encounters with a tool user. In short, as the number of tool-user encounters increases, so does the likelihood that a naive individual will acquire tool use (see learn sub-model). ***Under the conditions of genetic inheritance***, the acquisition of the tool-use trait is linked to reproduction (see reproduce sub-models). Naive individuals only become knowledgeable during birth, if a parent agent passes the tool-use trait to the offspring during a reproductive event. ***Under asocial conditions,*** individuals acquire the tool-use trait independently of their interactions with other agents. Instead, there is a fixed probability that an agent will acquire the tool-use trait and the end of each time step. Moreover, the asocial model also investigates how the preferential attraction of tool users to fixed locations in the grid space influences associations between tool users and non-tool users. The model reaches fixation when 50% of the individuals become knowledgeable.

**Entities, State Variables, and Scale**

***Global Environment***

The model is spatially explicit and, thus, is comprised of a 2-dimensional 20 x 20 grid cell space. The 2-D space is *not* wrapped into a torus. The space is inhabited by a single type of agent called Monkeys. Monkeys move through this space interacting, reproducing, and learning from other individuals. During the social and genetic inheritance conditions, each Monkey will age and eventually die at which point they are removed from this grid space. To prevent runaway population growth, the space can only be inhabited by a maximum of 100 individuals at a time. Time is represented with discrete time steps. Each time step is equal to the time required for a Monkey to move 1 grid cell, socially interact, or reproduce with another Monkey agent.

The global environment also possesses a variety of attributes and methods that monitor dynamics between individuals throughout the simulation. Attributes include *height, width, Na, N\_Starting\_Tool\_Users, transmission\_mode, run\_id, datetime, model\_stop, node\_data, and running timestep, N\_resources, learn\_rate, .* Methods include *computer\_n\_users* and *compute\_n\_w\_trait.*

*Attributes*

*height:* An integer value that determines the height of the grid space

*width:* An integer value that determines the width of the grid space

*Na:* An integer value that determines the number of agents that inhabit the grid-

space. This attribute is also used to determine the maximum number of Monkey agents that can exist on the grid space at once.

*N\_Starting\_Tool\_Users:* An integer value that determines the number of individuals who possess the tool-user skill at the beginning of the simulation.

*transmission\_mode:* A string value that determines the mode through which the tool use trait is transmitted. Can either be set to “social” or “inherited”. See sub-models learn and reproduce.

*run\_id:* A randomly generated six-character alphanumeric string that acts as the unique identifier for a specific run.

*datetime:* The specific time and date of the simulation. It is recorded at the beginning of the simulation

*model\_stop*: Initial coded as -1, this is replaced with the specific reason the simulation ended. The simulation can end when (1) 50% of individuals have acquired the tool-user skill or (2) all tool users have died and the tool-use skill can no longer be passed between individuals.

*running:* A true/false statement indicating whether the simulation is running.

*timestep:* An integer value indicating the current time step of the simulation

*node\_data*: A dictionary or data frame containing information regarding each Monkey in the simulation.

*social\_links:* A dictionary or data frame that serves as a record of any time an individual inhabited the same grid cell as another individual.

*n\_users:* An integer value corresponding to the current number of individuals that have acquired the tool-user skill.

*asocial\_rate:* An integer value (1-100) corresponding to the likelihood that an agent will acquire tool use during asocial conditions (for asocial conditions only).

*attraction\_strength:* An integer value (1-100) corresponding to the likelihood that an agent will move in the direction of the nearest attractor (for asocial conditions only).

*Methods:*

*compute\_n\_tool\_users:* Returns the current number of living individuals that are tool-users as an integer value.

*compute\_n\_w\_tool\_trait*: Returns an integer value corresponding to the current number of individuals that have inherited the tool-use trait.

***Monkey-Agent***

Monkeys represent individuals within a single coherent group of hybrid Long-tailed Macaques. Like wild macaques, Monkeys (aka Monkey-agents) forage, and interact with one another for social, learning, and reproductive purposes. Moreover, Monkeys also age and die, throughout the simulation. These behavioral capacities are reflected in the 6 methods they can execute: *d2\_mother, move*, *grow*, *reproduce, social interaction,* *learn, step* (see descriptions of each in the Submodels section below). Monkey agents possess 15 state variables: *id, pos, tool\_user, tool\_trait, learned\_tool\_use, age, age\_learned\_tool\_use, ts\_learned, transmission\_method, living, tool\_user\_encounters, prox\_associations, mother, mother\_tool\_user, hair\_pattern*

*Attributes*

*id:* An integer value that acts as a unique identifier for the agent. All agents within the Mesa modeling framework are automatically assigned an *id*.

*pos:* A tuple representing the current location of the agent in the grid space as (x,y) coordinates. All agents within the Mesa framework are automatically given the attribute

*pos.* See **initialization** and the submodel *reproduce* for how coordinates are initially assigned to the *pos* attribute.

*tool\_user:* A true/false statement that indicates whether the agent is a tool-user or not

*tool\_trait:* A true/false statement that indicates whether the individual inherited

the tool use trait (See *reproduce* submodel*)*.

*learned\_tool\_use:* A True/False attribute that indicates whether the individual has learned.

*age*: A non-negative integer value that represents the number of time steps that an individual Monkey agent has been alive for (see *grow* submodel).

*age\_learned\_tool\_use:* A non-negative integer value indicating the age of the agent when it became a tool user.

*ts\_learned:* A non-negative integer value indicating the time step that the agent becomes a tool user.

*transmission\_method:* Indicates whether the tool used was acquired via social learning or inheritance processes. It is set to either “social” or “inherited”. When the agent has not yet acquired the tool use this variable is set to “Naive”.

*living:* A True/False attribute that indicates whether the agent currently exists in the grid space (see *grow* submodel).

*tool\_user\_encounters:* A non-negative integer referring to the number of times an individual has shared the same location as a tool user.

*prox\_associations:* A non-negative integer corresponding to the number of times the agent has shared the same grid cell as another individual.

*mother:* The unique identifier of the Monkey-agent that gave birth to this Monkey-agent

*mother\_tool\_user:* A True/False attribute that indicates whether the mother of the agent was a tool-user.

*hair\_pattern:* An integer value of 1 or 2 that defines the monkey-agent’s phenotype. Individuals with a value of 1 are implied to be phenotypically distinct from Monkeys that possess a value of 2.

*Methods: (See sub-models for detailed descriptions).*

*d2\_mother:* Calculates the distance from the agent’s current location to the location of the mother (see attribute *mother*).

*move:* Determines which grid cell the agent moves into during each timestep.

*social interaction:* The function responsible for logging instances when the agent encounters another agent in the grid cell it just moved to.

*reproduce:* The function responsible for initiating reproductive events. This includes generating new agents (offsprings) and whether the tool-use trait is passed from parent individuals to the offspring.

*learn:* Determines whether an individual acquires the tool-use skill.

*grow:* A function that controls the aging process of the agent. During each time step, it increases the *age* of the agent by one and determines whether the agent- dies

*step:* Responsible for executing the aforementioned methods in each time step. For further details, refer to the section on process overview and schedule.

***Attractor-Agent*** (asocial conditions only)

Attractor agents serve as locations that tool users are attracted to. They possess a single state variable: *pos*

*Attributes*

*pos:* A tuple representing the current location of the agent in the grid space as (x,y) coordinates. All agents within the Mesa framework are automatically given the attribute

*pos.* See **initialization** and the submodel *reproduce* for how coordinates are initially assigned to the *pos* attribute.

**Process Overview and Scheduling**

*Social Inheritance and Genetic inheritance*

During each time step, every Monkey agent executes a series of methods (see above). The order in which each agent is asked to execute its behaviors is determined by random activation. During each time step, the active agent will move a unit of 1 grid cell (*move*). After the agent moves, it determines if other agents occupy its new location (*social\_interaction)*. If this is true, then the encounter with the other agent is recorded by the global environment. Sharing a grid cell with another individual also facilitates a chance for reproduction to occur (See *reproduce* submodel). The reproduction method is only triggered if the number of agents that exist on the grid space is less than the population limit (*Na)*. Reproduction results in the generation of a new Monkey agent (Offspring). A subset of the Monkey’s attributes is modified according to the social interaction and reproduction methods. The agent will then have an opportunity to become a tool user via the *learn* method. The criteria for becoming a tool user are determined bythe *transmission\_method* set by the global environment (see *learn* submodel). Finally, the Monkey will *grow*, meaning that the Monkey’s age will increase by a one-time step. There is also a chance that the agent will die. If death occurs, then the agent is removed from the grid space (See Grow Submodel).

*Asocial Conditions*

The general mechanics of this condition are identical to the social and genetic inheritance conditions except in two ways. (1) Agents do not reproduce. (2) Agents do not age or die. As a result, the population is comprised of the initially generated agents throughout the simulation.

**Design Concepts**

Emergence

Emergence is observed in the social networks that arise due to individual agents encountering each other (sharing the same grid cell) throughout the simulation. This is not planned but instead dictated by the movements of individual agents during the simulation. In addition, social relationships between tool-users and non-tool-users due emerge due to the aggregation of individual social and reproductive interactions between individuals.

Stochasticity

Stochasticity can be found in many places throughout the initialization and implementation of the model. During initialization, 100 Monkey agents arerandomly placed in the grid space. The age of these initial 100 agents is determined by randomly drawing from a uniform distribution of values between 0 and 100. In addition, 1 of the initial Monkey agents is randomly set as a tool user. Stochasticity also plays a prominent role in the movement of the Monkey Agents. Monkey agents move according to Brownian or a modified version of Brownian motion (see *move* submodel). The death of each agent is randomly determined by drawing from a binomial distribution (See grow submodel).

Collectives

The interactions between agents, when taken, as a whole, can be considered a collective as it is a social network reflecting relationships between individuals at the group level.

Observations

Data are collected at the end of each simulation run, which is marked by 50 percent or more of the living individuals who have acquired the ability to use tools. When the simulation ends, data regarding the individual agents is exported as a CSV file. The record of social interactions between individual monkeys is also exported as a CSV file. Note that all of the data analysis is done in R, not in Mesa.

**Details**

Initialization

Each simulation begins by creating 100 Monkey-agents that are randomly distributed across the grid space. The x and y coordinate (*pos* attribute) of each agent is set by randomly drawing from a uniform distribution with a minimum value of 1 and a maximum value of 25 (the boundaries of the grid space). The age of these initial 100 Monkeys is set by randomly drawing from a uniform distribution of values between 0 and 450. This prevents mass die-off events as the initial population of individuals ages. For these initial 100 individuals, the attributes *mother* and m*other\_tool\_user* are set to “unknown”. See the *reproduce* submodel for how these attributes are set in monkey-agents generated after the initialization phase of the simulation. The *hair\_pattern* attribute is set by a random choice between the integers 1 and 2.For 1 randomly chosen individual with a *hair\_pattern* of 2, the *tool\_user* attribute is set to True. The attribute *tool\_user* is set to *False* for the remaining 99 individuals. The simulations do not require any input files. If the *transmission mode* is set to asocial, then attractor agents are also randomly distributed across the grid space. The number of attractors is determined by the *n\_attractors* variable.

**Data Collection**

At the end of each simulation run, data recorded during each simulation is exported as three separate CSV files: run\_data.csv, nodes.csv, and social\_edges.csv. The run\_data.csv contains the information for the attributes of the global environment for the simulation. This file contains a column for the following attributes: *run\_id, datetime, height, width, N\_Starting\_Tool\_Users, Na, Transmission\_method,* and, *model\_stop*. The nodes.csv file contains information for each monkey agent in the simulation. For each monkey agent, we collect *id, living, tool\_user, learned\_tool\_use, tool\_user\_encounters, age\_learned\_tool\_use, age\_learned\_tool\_use, ts\_learned, learning\_method, age, mother, mother\_tool\_user,* and *hair\_pattern.* The social\_edges.csv contains a record of all interactions that occurred between Monkey agents during the simulation. Recall, that social interactions occur when individual agents share their current grid cell with another agent. These interactions are recorded in a data frame with two columns named source and target (see *social \_interaction* submodel.

**Submodels**

*move:* This submodel changes the location of the agent according to a modified version of Brownian motion. The modifications to Brownian motion, depending on the model condition that is simulated.

*Social and Genetic inheritance conditions*

The agent identifies its 8 neighboring grid cells and then randomly chooses one of these grid cells to move into. The *pos* attribute is then updated with the XY coordinates of this location. To simulate the fact that younger (infants and juveniles) primates will be spatially associated with their mothers throughout development (Lonsdorf, 2013). The choice of which grid cell to move into is weighted by the location of the mother (see *reproduce* submodel for how the mother agent is determined). Grid cells that minimize the distance from the agent to their mother are more likely to be chosen. The decision to move to a grid cell that brings an agent closer to or to the same location as the mother is determined by randomly drawing from a binomial distribution. If the value is 1 then the agent chooses a grid cell that minimizes the distance between the mother and the agent. If the value is 0 then the choice is random. The probability (*p*) that the value of 1is returned is determined by *1-((2 x age)/100).* Thus, the influence of the mother’s location where the agent moves weaken exponentially as the agent gets only. If the calculation returns a negative value then *p* is automatically set to 0. By the time the agent possesses an age of 50 time-steps, their movement is no longer influenced by the mother’s location.

*Asocial conditions*

In addition to the mechanics outlined above, agents, that possess the tool-use trait, will also move according to attractor locations. During this, agents will identify the location of the nearest attractor. The agent will then draw from a binomial distribution where the probability of success is equal to the variable *attractor\_strength*. If success is drawn from the binomial distribution, then the agent will move into the grid cell which minimizes the distance between its current location and the attractor.

*d2\_mother:* This is a helper function for the move method. It calculated the distance of each grid cell that the agent could move to and then returns the grid cell that is closest to the mother of the agent.

*social\_interaction:* This sub-model determines whether an agent occupies the grid cell that the active agent has just moved into. If this is the case, the *prox\_associations* attribute of the active agent is increased by 1. If the agent already occupying the grid cell is a tool user, then the *n\_tool\_user\_encounters* attribute also increases by 1. Finally, the social\_edges.csv is updated listing the agent that has just moved into the grid cell as the target and the agent already occupying the grid cell as the source. If more than one agent occupies the grid cell then the agent randomly chooses who to interact with.

*learn:* The learn submodel determines if the agent who has just moved into the grid cell will acquire the tool-use skill from the individual occupying the square. Agents are only eligible to learn tool use when their age is greater than or equal to 25 time steps. This simulates the developmental period over which tool use emerges in long-tail macaques (Tan, 2017). When social learning is permitted (Global attribute *Transmission\_mode =* “social”*),* the agent has a chance to acquire tool-use from the individual already occupying the grid cell provided they are a tool-user themselves (*tool\_user* = True*)*. The probability that the Monkey agent acquires the tool-use skill is determined by drawing from a binomial distribution. Again, *p* is determined by the number of previous encounters with a tool user *n\_tool\_user\_encounters*. Thus, *p* is equal to *n\_tool\_user\_encounters / 100.* Therefore, each encounter with a tool user increases the chance of becoming a tool used by 1 percent.Under conditions of inheritance, the agent becomes a tool user once their *age* is greater than or equal to 25. If the Monkey agent acquires the skill then the attribute *tool\_user* is changed from False to True.

*reproduce:* This method simulates a reproductive event between two agents. This results in the generation of a new Monkey Agent (offspring). The new Monkey agent is placed at the location where the *reproduction* method was triggered. The *pos* attribute for the offspring agent is, thus, updated with the (x,y) coordinates that correspond with this location. Its *age* attribute is set to zero. *Tool\_user* is set to false. The *mother* attribute is assigned the id of the agent that triggered the *reproduce* method (i.e. the active agent). *Tool\_using\_mother* is set equal to the t*ool\_user* attribute (True/False) of the agent that is defined as the mother. The *hair\_pattern* attribute is determined by the *hair\_pattern* values of the parent agents. If both parent agents possess a *hair\_pattern* of 1 then the *hair\_pattern* of the offspring is set to 1. If both parent agents possess a  *hair\_pattern* of 2 then the *hair\_pattern* of the offspring is set to 2. In the case, that one parent possesses a *hair\_pattern* of 1 and the other a *hair\_pattern* of 2. Then the *hair\_pattern*  of the offspring is determined by a random choice between the values of 1 and 2.

The *tool\_use\_trait* of the offspring agent depends on both the *tool\_use\_trait* attribute of the parents **and** the *hair\_pattern* value inherited by the newly generated offspring agent. The *tool\_use\_trait* attribute will only be set to True if one of the parents possesses the *tool\_use\_trait* and the *hair\_pattern* inherited by the offspring is 2.

*grow:* When this function is triggered, the *age* attribute for the active monkey agent increases by 1. Following this, their function determines whether the agent will die. Death is determined by drawing from a binomial distribution. If the value returned is 1 then the agent dies. If the drawn value is 0 then the agent lives. The likelihood of drawing a value of 1 (*p*) is determined by a baseline probability of 1e-4 plus the age of the agent divided by 1e-4.

*step* This submodel executes the aforementioned models in the following order.

(1) *move*

(2) *social\_interaction*

(3) *reproduce*

(4) *learn*

(5) *grow*

**Contact Information**

Jonathan Reeves designed and programmed this model. Please feel free to share any comments, suggestions, corrections, or critiques with them at these addresses:

Jonathan Reeves

Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

Jonathan\_reeves@eva.mpg.de

**References**

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: A review and first update. Ecological Modelling. 221, 2760–2768.

Lonsdorf, E.V., 2013. The Role of Mothers in the Development of Complex Skills in Chimpanzees. In: Clancy, K.B.H., Hinde, K., Rutherford, J.N. (Eds.), Building Babies: Primate Development in Proximate and Ultimate Perspective, Developments in Primatology: Progress and Prospects. Springer, New York, NY, pp. 303–318.

Masad, D., Kazil, J., 2015. MESA: An Agent-Based Modeling Framework. Proceedings of the 14th Python in Science Conference (SCIPY 2015). 53–60.

Tan, A.W.Y., 2017. From play to proficiency: The ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-action perspective. Journal of Comparative Psychology. 131, 89.