Online Supplement 1, ODD Protocol Model Description, for:

Investigating the costs and benefits of gregarious foraging

Authors:

Ekanayake-Weber, Marcy; Mathew, Namita; Cunha, Deanna; Payen, Nathanael; Grimm, Volker; Koenig, Andreas.

1. Purpose and patterns

The purpose of this model was for the theoretical exposition of the costs and benefits of group living in primates. Specifically, the model was built to explain the impacts of gregariousness (i.e., the behavioral inclination to aggregate with conspecifics) on feeding competition, and how these impacts are mediated by interacting resource characteristics.

The model was calibrated and validated using patterns derived from field data for a wide variety of primate species. Two key patterns of primate foraging behavior, daily path length (Vidal-Cordasco et al., 2020) and activity budget (Kamilar and Cooper, 2013), were derived from recent comparative studies. Though there are methodological concerns with such data (e.g., see (Patterson et al., 2014), here they were only used to decide what range of parameter space to focus on within the model, rather than matching exactly the characteristics of any one species. Daily path length for primates was observed to vary from less than 200 meters per day (*Eulemur fulvus fulvus*), up to extremes of 6 km (*Macaca nigra*), 8.6 km (*Papio hamadryas*), and 10 km (*Homo sapiens*), with 97% of species falling between 0.25 and 4.0 km per day (Vidal-Cordasco et al., 2020). The ratio of time spent moving versus eating also varied widely, from 0.067 to 0.77 (Kamilar and Cooper, 2013). For approximately 85% of primate species (59 out of 70 species for which activity budget data was available), the ratio of time moving:eating was between 0.25 and 0.6 (Kamilar and Cooper, 2013). Using data from preliminary runs, we calibrated our model to focus on the parameter space which generated daily path lengths between 0.25 to 4.0 km and moving:eating ratios between 0.25 to 0.6 (see online supplement 2 for further details).

2. Entities, state variables, and scales

The entities of this model were primates and resource patches.

Primates were the agents of the model. The state variables characterizing primates are listed in Table 1. Primate agents did not have any sex or age assigned.

Space was represented continuously for primate movement, but was subdivided into discrete patches for representing resources. The simulated landscape consisted of a square torus (wrapping horizontally and vertically) of 281 by 281 patches (i.e., 78,961 patches total). Each patch was intended to approximately represent a 10m x 10m area of habitat, or, a single tree canopy (as in (Chapman et al., 1995a). Therefore, the entire landscape represented an area of 2.81 x 2.81 km, or, 7.9 square kilometers. Resource patches were patches containing energy, i.e., feeding sites. All patches were characterized by their coordinates and the variables listed in Table 1. More than one primate could occupy a patch, but patches were "usurpable" (Isbell and Young 2002), meaning one primate could try to exclude another from the patch they co-occupied.

For the sake of realism, we varied the agent population size in proportion with resource abundance, but allowed this proportion to vary. Thus, there were two parameters that determined population size: resource abundance (total amount of energy distributed on the landscape) and energy per capita (amount of energy for each primate agent). With resource abundance varying between 200,000 and 1,200,000 energy units, and energy per capita varying between 4,000 and 9,000 energy units, the population size varied from 22 agents to 300 agents. With the spatial scale mentioned above, this resulted in primate densities ranging between 2.8 individuals per km^2 to 38.5 individuals per km^2.

The model was represented in discrete time steps. Each "tick" (i.e., turn) corresponded to approximately 30 minutes of daylight time. Thus, 24 ticks represented the events which would take place over the daylight hours of one day, assuming equal day and night time hours and ignoring potential effects of seasonal variation in day length. The simulations ran for 4,300 timesteps, which represented approximately six months.

3. **Process Overview and scheduling**

Different processes were run at different time scales in the model.

Half-hourly

Within each time-step representing half an hour, the following events took place in the following order.

1. Each primate would assess whether the current patch they occupied contained any energy, and then either eat or move.
    a. If the current patch contained energy, the “eat” procedure was called. Before consuming energy from the patch, the primate would sense whether there were other co-occupants of the current patch, and decide whether to try to displace one of them (“decide_to_fight”; see submodels below). After this decision, if the primate had not been chased out of the patch as a result, they would consume a set amount (“extraction-rate”) from the patch. Then their actions were complete for this time-step.
    b. If the current patch was depleted of energy, the primate would sense other nearby primates (“find_nearest_primates”), and also sense nearby resource patches (“find_visible-resources”). Then, the “move” procedure was called. Movement involved a combination of maintaining gregariousness rules and moving towards the highest-energy patch. This is described in more detail below in the Submodels section.
2. After all primates had either eaten or moved, each primate had their memory of previous fight wins and losses decay by the appropriate amount, depending on whether their current exp-score was above or below the running average (see below, submodels).

Variably Occuring

On a longer timescale, resource patches would regrow. The patch regrowth interval was controlled by a parameter, “patch-regrowth-interval,” so that it could vary and its influence could be assessed. Patch-regrowth-interval was the latency to regrow; when patch regrow interval was 500, patches could regrow every 500 timesteps, representing a landscape with renewing and/or seasonally alternating food sources. When patch regrow interval was set to 3000, patches could only regrow every 3000 timesteps. Thus, a higher patch regrowth interval meant that resources remained depleted for longer stretches of time.

4. Design Concepts

Basic Principles

This model addresses the way in which the costs and benefits of gregariousness are influenced by the characteristics of food resources. Prevailing hypotheses posit that animals which forage socially (such as most anthropoid primates) should experience feeding competition proportionate to the number of other conspecific foragers present, and that this competition is one of the principal costs associated with group living (e.g., (Alexander, 1974; van Schaik, 1983; Janson, 1988). Previous agent-based models (Ruxton, 1995; Beauchamp, 2005) have illustrated that, on simple landscapes, group foragers have lower foraging efficiency, but also lower variance in energy intake. However, feeding competition is known to be heavily influenced by many interacting resource characteristics, including abundance, extraction rate, patch distribution, and patch size (Isbell and Van Vuren, 1996; Koenig and Borries, 2006). Thus, these elements were included in our model. For the sake of simplicity, agents did not behave according to optimal foraging theory (Mangel and Clark, 1986); resource extraction from a patch was constant until a patch was completely depleted, at which point all occupants would move.

Emergence

How much energy the primate could gain was the emergent result of their decisions on movement and fight decisions or, with other words, of both direct and indirect competition with other primates, the properties of the landscape, and the gregariousness rules that the primate was obeying. The decision rules were based on implicit assumptions about fitness consequences. The repeated interactions between landscape and behavior allowed travel distances and trajectories to emerge, as well as metrics of foraging efficiency.

Adaptation

Agents had three adaptive behaviors. First, if the patch they were currently on did not contain any energy, the agent would decide to leave the patch and attempt to locate a patch with a high amount of energy. Alternatively, while on a patch containing energy, the agent could decide whether to attempt to fight one of the other agents co-occupying that patch, in order to gain a larger portion of the patch's energy (see Submodel below, Deciding to Fight, Fighting, and Exp-score). Both of these adaptive behaviors sought to maximize energy intake (see Objectives, below). Finally, an agent would decide to forgo resource foraging in order to maintain proximity to other agents, if its gregariousness rules were not met. This adaptive behavior sought to satisfy (rather than maximize) the objective of the gregariousness rules.

Objectives

The primate had the competing objectives of 1) gaining the maximum amount of energy and 2) maintaining a certain distance from a certain number of other primates. The agents' maximizing objective was to accumulate the most energy, which was implicitly linked to real-world survival, reproductive success, and fitness. Agents expressed this in two ways: moving towards high-quality resource patches, and attempting to exclude other primates from their current resource patch (see submodel below, Deciding to Fight, Fighting, and Exp-score). By contrast, the gregariousness rules were a satisficing objective, which only altered the behavior of the agents when certain conditions were met (see submodel below, Movement Decisions).

Learning

Through exp-scores, primates learned their own and others' fighting abilities through memory of past conflicts. With more experience, primates were able to make more accurate predictions of who will win or lose future conflicts (see submodel below, Deciding to Fight, Fighting, and Exp-score). Agents did not learn or remember the locations of resource patches or clumps.

Prediction

Agents attempted to accurately predict the outcome of a possible fight before deciding to attack another agent. If the agent predicted that they would lose, they were less likely to decide to attack. This prediction was done using the attribute "exp-score" (see submodel below, Deciding to Fight, Fighting, and Exp-score).

Sensing

Primates sensed information about the environment, themselves, and other primates.

Primates sensed the location of resource patches within the zone of resource-detection-patch-radius, and they could sense the relative current energy contents of these patches. Primates could also sense the current location of other nearby primates within other-primate-detection-radius, up to the count of the current tgt-neighbor value (see table 2 and submodels). Primates could also sense the exp-scores of themselves and primates on the same patch as themselves. Exp-scores were reflective of a "memory" of past aggressive encounters, and were used to estimate the costs of engaging in a future encounter (see Submodels below, Deciding to Fight, Fighting, and Exp-score).

Interaction

Primate interacted both indirectly and directly in this model. Primates interacted indirectly by consuming resources. If the patch's energy was greater than zero, then the primate could consume an amount determined by the patch's extraction-rate. This energy was then unavailable to other primates until the patch could regrow.

Primates directly interacted according to their gregariousness rules. When they did not have the "target neighbor" amount of other agents within the radius of the target distance, then the agent would move towards the average location of the primates that were visible to them (within other-primate-detection-radius). Primates also directly interacted by fighting to try and evict each other out of a shared patch (see submodels below, Deciding to Fight, Fighting, and Exp-score).

Stochasticity

Processes driven by pseudorandom numbers were the following. At initialization, the assignment of each patch's energy contents was drawn from a normal distribution defined by the parameters qual-mean and qual-sd, and the assignment of each patch's extraction rate was drawn from a normal distribution controlled by the parameters extraction-rate-mean and extraction-rate-sd. During the movement procedure "wander" (and "travel" when target neighbor was 0), the agent made small turns right or left according to a randomly-generated number between 0 and the parameter "movement-noise." The decision to attack another agent was also determined by a randomly-generated value between 0.0 and 1.0 (see submodel below, Deciding to Fight, Fighting, and Exp-score).

Collectives

While following gregariousness rules, agents would form emergent spatial aggregations of agents which could be considered as collectives. Clumps were collectives of resource patches, whose size determined the overall resource distribution of the simulated landscapes.

Observation

The model's outcomes were observed through a few summary variables. For hypothesis 1, we observed foraging efficiency (energy gained divided by distance traveled, averaged across the population), energy intake rate (energy gained divided by ticks, averaged across the population), and daily distance traveled (distance traveled divided by (ticks divided by 24), averaged across the population. For hypothesis 2, we observed quarterly variance in energy intake, and biweekly variance in energy intake.

5. Details

Initialization

The "setup" procedure initialized each unique simulation of the model. The starting conditions of each simulation were controlled by a number of resource parameters (Table 2, Figure 1). A resource landscape of 281 x 281 patches was created, according to the parameters settings on the Graphical User Interface, a BehaviorSpace experiment (a NetLogo tool to define simulation experiments; Wilensky and Shargel 2001), or a simulation experiment defined and run from R using the nlrx package (Salecker et al., 2019). The setup procedure would create new clumps of resource patches (using the parameter "clump-size") and fill in resources patches in these clumps (using the parameters "qual-mean" and "qual-sd") until the total desired amount of energy was distributed on the landscape (as prescribed by the parameter "abundance"). Clumps could overlap, in which case very dense "super-clumps" would form, and any "leftover" energy from a clump whose area already had many patches filled in would simply be distributed in another new clump. The primate population size was calculated by dividing the resource abundance by the energy-per-capita. Then, that amount of primate agents were produced, each assigned a resource holding potential between 1 and 8, and placed on one of 5 randomly-selected resource patches from across the entire landscape. Primates began on this limited number of spawn points so that they did not have to search randomly for resources at the very beginning of the simulation, nor search for other agents, which could have artificially inflated the variance in distance traveled and foraging efficiency.

Input data

The model does not use input data to represent time-varying processes.

Submodels

All model parameters are listed in OS1 Table 2.

Movement Decisions

Agents would move when the patch they were occupying no longer contained any energy. Agents did not pay any explicit cost for movement, in terms of energy. However, we focused on foraging efficiency (energy intake divided by distance traveled) as our main foraging metric, since this incorporates both benefits and costs. Agents only responded to resources and other agents within their sensory range; they had no memory of the locations of previously-visited resources. In a single time-step, agents could move as many patch distances as the parameter “max-move” indicated. Agents could also take steps that were shorter than max-move, if the selected destination patch was less than max-move patch distance away. Before taking a “step”, agents would decide how to adjust their heading. This was a combination of being attracted to the highest-value patches and obeying gregariousness rules (see Figure 2).

Wander and travel. If there were no resource patches within the sensory range of the agent (resource-detection-radius), and there were no other agents detected nearby *or* target neighbor = 0, the agent would have their heading changed a random amount as limited by the parameter movement-noise (corresponding to a correlated random walk; procedures "wander"/"travel" when target neighbor = 0). If there were no resource patches within sensory range but there were other agents nearby *and* target neighbor was ≥1, then the agent would change their heading to be the average direction towards all visible conspecifics (procedure "travel").

Forage. The agent had satisfied their gregariousness rules if they had the appropriate number of neighbors (set by target neighbors) within the appropriate distance (set by target distance; see Figure 2 A, B, D). If both conditions were met, the agent would adjust their heading towards the patch with the most energy within their sensory range (procedure "forage"). While moving for multiple timesteps in a row, agents would maintain the same goal patch ("patch-picked") rather than picking a new destination each timestep, so long as the patch-picked was still within sensory range.

Cohere. If target neighbor ≥ 1 and the agent did not have enough target neighbors within the target distance, then the agent would ignore resources in favor of attempting to fulfill its gregariousness rules (procedure "cohere"; see Figure 2C). If there were other agents within sensory range but outside the target distance, the agent would adjust their heading to be directed towards the average location of visible other agents. If there were no other agents sensed outside of the target distance, the agent would revert to foraging (see above) for that timestep. If target neighbors = 0, the agent would only wander and forage.

Deciding to Fight, Fighting, and Exp-score

If the patch that an agent was occupying at the beginning of their turn contained energy, then the agent had the option to try to fight one other agent occupying the same patch (see "Schedule" above). As an outcome of a fight, the loser was forced to "flee" the patch. Therefore, it was in each agent's best interest to evict weaker agents out of a patch to avoid having to share food, but to not start fights which they would lose, since this would deprive themselves of the resource. Agents made this choice using a procedure called “decide_to_fight,” which was greatly influenced by the design of previous models including DomWorld (Hemelrijk, 1999, 2000) and the earlier MIRROR modeling methodology, developed for bee behavior (Hogeweg and Hesper, 1983, 1985). Detailed testing of this aspect of the model is described in Ekanayake-Weber et al. in review, The American Naturalist. Upon selecting an opponent randomly from the other patch occupants, the agent would estimate benefits of fighting (how much more energy they were likely to gain with the opponent evicted) and the costs of fighting (comparing exp-scores, based on the history of previous fights; see below). Costs were estimated to be high if the opposing agent was particularly strong (high exp-score) and/or the approaching agent was weak (low exp-score); conversely, costs could be estimated to be low if the approaching agent appeared strong and/or the opposing agent appeared weak. costs of attacking were estimated as:

$$C = \frac{exp{-}score_{opp} - exp{-}score_{self} + 1}{2}$$

Equation OS1.1. Costs estimation for experience-based decision-making.

The formula was designed to vary between 0.0 and 1.0. When opponents were equal ($exp\text{-}score_{opp}$ - $exp\text{-}score_{self}$ = 0), the formula was designed to return a cost estimation of 0.5.

To compare the benefits and cost estimations, costs (*C*) and benefits (*B*) were weighed equally, as both were put on a 0.0 to 1.0 scale. The decision to attack was stochastic, such that the likelihood of attack was

$$P(attack) = \frac{B}{B + C}$$

Equation 4. Cost-benefit analysis in the decision to attack.

Therefore, as the benefits increased relative to the costs, the approaching agent had a higher probability of attacking, and as the costs increased relative to the benefits, the approaching agent had a decreasing probability of attacking (see Figure 1). When costs and benefits were equal (whether low or high), the chance of attacking was 0.5.

If the agent decided to fight the opponent (as described above), then the winner was determined based on the two agents' resource holding potentials (RHPs). RHP represented the overall fighting ability of the agent, which in many species is a combination of body size, body weight, agility, fighting experience, and weaponry, among other factors. RHP was assigned randomly to all agents at the beginning of each simulation, and had a value between 1 and 8 which did not change during the simulations. The winner of the fight was always the agent with the higher RHP. If two agents had the exact same RHP, then the aggressor would lose the fight.

After each fight, the combatants had the opportunity to "remember" whether they had won or lost, using the variable "exp-score." Exp-score was an attribute that each agent possessed, always beginning at 0.5 and ranging from 0 to 1.0. When an agent won a fight, the exp-score was increased by 0.01 (unless the exp-score was already above 0.98). When an agent lost a fight, the exp-score was decreased by 0.01 (unless the exp-score was already below 0.02). Thus, repeated losses over time would lead to exp-scores << 0.5 and repeated wins would lead to exp-scores >> 0.5. It was in this way that agents assessed each other's competitive abilities, relative to their own. Exp-score also decayed over time towards a running average of the previous five fight outcomes.

Table OS1.1. Variables in the agent-based model, including agent attributes and patch attributes.

Category	**Variable name**	**Description**	**states/data structure**
Agent attribute	stored-energy	The amount of energy (in relative units) that the agent has accumulated; all agents start at 30	Real number (float)
	rhp	The competitive ability of the agent, assigned randomly at birth/initialization.	Integers 1-8
	nearest-primates	Primates within visual range (“other-primate-detection-radius”); if more than “tgt-neighbor”, limited to that number of primates	Turtle-set of primates
	visible-resources	Resources tiles currently containing energy within the visual range (resource-detection-radius)	Patch-set
	exp-score	current value of estimated fighting ability based on previous recorded fight outcomes	Float between 0.0 and 1.0
	exp-delta-list	List recording every time the exp-score was changed by a win or loss	List of floats
	xcor, ycor	Coordinates describing the current location of the agent	Float, float; range, -140 to 140
	heading	The current direction that the agent is pointing; 0 is north, 90 is east, etc.	Degrees out of 360 (clockwise)
Patch attribute	pxcor, pycor	Coordinates describing the location of the patch	Integer, integer; range, -140 to 140
	penergy	The current energetic contents of the patch	Integer; range depends on parameter values
	quality	The maximum energetic contents of the patch, up to which it regrows	Integer; range depends on parameter values
	extraction-rate	How much energy can be extracted from this patch per tick	Float; range depends on parameter values

Table OS1.2. Global model parameters set by sliders in NetLogo's interface tab, and analyzed by Morris Elementary Effect analysis.

Category	Parameter	Description/Interpretation	Range of values	MEE?
Gregariousness	tgt-neighbor	The number of neighbors that each primate must have within the target distance	Integer between 0 and 11	all
	tgt-distance	The target radius that each primate must maintain a targeted number of primate neighbors within	1 to 49 patch-distances	all
Resource characteristics	abundance	Total amount of energy units to be distributed across the landscape	200,000 to 1,200,000 energy units	all
	energy-per-capita	Energy units distributed for each primate agent created. Population size calculated by dividing abundance by/ energy-per-capita.	4,000 to 9,000 energy units	all
	clump-size	The mean of the normal distribution which determines the number of patches in a clump	Integer between 0 and 500	all
	qual-mean	The mean of a normal distribution which determines energy in patch	Integer between 25 and 150	all
	qual-sd	The standard deviation of a normal distribution which determines patch qualities	Integer between 1 and 20	Pattern-matching only
	regrowth-rate	The amount of energy gained by each patch in the landscape at a certain frequency	0.5 to 1.0 of quality regrown every patch-regrowth-freq	Pattern-matching only
	patch-regrowth-interval	The interval at which patches have the ability to regrow; longer intervals mean less frequent regrowth/more variability over time in resource availability	Integer between 500 and 3000 time-steps	all
	Extraction-rate-mean	The mean of a normal distribution which determines how much energy a primate can extract from a particular patch in single time-step (i.e., determines depletion speed of patch)	2 to energy units per time-step	all
	Extraction-rate-sd	The standard deviation of a normal distribution which determines how much energy a primate can extract from a particular patch in a single time-step	0 to 3 energy units per time-step	all

Primate movement and sensory characteristics	movement-noise	A number that is used to add randomness to a primate's heading when wandering, traveling or dispersing; this is done by subtracting a half of movement-noise from a random number selected from 0 to movement-noise and adding to the primate's heading	10 to 45 degrees	Pattern-matching only
	max-move	The maximum distance that a primate agent can travel in a single time step.	10 to 50 patch-distances for pattern-matching; 25 to 50 patch-distances for hypothesis testing	all
	resource-detection-radius	The radius within which a primate can detect all patches with energy units greater than 0	50 to 100 patch-distances	Pattern-matching only
	Other-primate-detection-radius	The radius within which a primate can detect other neighboring primates	50 to 100 patch-distances	Pattern-matching only