

# EPICURE: An Agent-Based Foraging Model

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## Abstract

We present an agent-based foraging model, EPICURE, which captures the results from recent human group foraging experiments (Goldstone and Ashpole, 2004; Goldstone et al., 2005), provides a novel explanation for those results and previous animal foraging results, and makes predictions for future foraging experiments. We describe a series of simulations that test the sources of resource undermatching often found in group foraging experiments. We conclude that foraging group size, food rate, and spatial distribution of food interact to produce undermatching, and occasionally, overmatching, to resources. Furthermore, we present wealth distribution results from the aforementioned empirical studies and EPICURE simulations.

## Introduction

Animals often forage for resources and even mates in groups. By congregating with others, individuals can acquire social sampling information and learn new strategies in order to improve food intake and mate selection rates, but these advantages can be compromised by member competition and density-dependent interference and perceptual limitations. In this paper, we describe an agent-based model that captures the interplay between individuals' foraging strategies and the emergent group foraging behavior.

Group foraging distributions are often compared to the ideal free distribution (IFD) model (Fretwell & Lucas, 1970), which predicts that a group of foragers will distribute themselves to resource patches in proportion to the relative resources available at each patch. In an environment where one resource pool holds 80% of the resources while a second pool holds the remaining 20% of resources, the IFD predicts that a group of foragers will optimally distribute themselves to the resource pools, with 80% of the foragers in the first pool and 20% in the second pool. However, many experiments report systematic undermatching in which fewer than expected foragers attend the more profitable patch while more than expected foragers attend the less profitable patch. Undermatching has been found in cichlid fish (Godin and Keenleyside, 1984), zebrafish (Gillis and Kramer, 1984), pigeons (Baum and Kraft, 1998), and humans (Goldstone et al., 2005). In a meta-analysis of undermatching in animal foraging studies, Kennedy and Gray (1993) conclude that information regarding the "relative and absolute resource

availability, number of animals, perceptual abilities of animals, competitive interactions, competitive abilities of animals, and the effects of travel between sites" (p. 165) may all lead to undermatching and violate the IFD.

Goldstone and Ashpole (2004) examined group foraging behavior among humans by developing an experimental networked Java platform to create a common two-dimensional virtual world (an 80 x 80 grid) across computers. Participants sat at their respective computers and foraged for resources in real time by using the computers' arrow keys to move up, down, left, and right in order to step on a food pellet and thereby consume it. We will briefly describe the experimental manipulations because their foraging environment and data serve as the initial basis for our agent model. Participants engaged in 6 five-minute sessions, consisting of all combinations of two perceptual conditions and three resource distribution conditions, and all participants experienced the same conditions in a given session. In the "visible" perceptual condition, a participant could see himself or herself as a yellow dot in the virtual world, and other participants were visible as blue dots while available food pellets were represented as green dots. The visible condition is therefore a good match for the assumptions of IFD (Fretwell and Lucas, 1970). In the "invisible" perceptual condition, a participant could see himself or herself as a yellow dot in the virtual world, but no other participants or food were visible in the world. The invisible condition corresponds to foraging experiments with sampling under uncertainty. The visible and invisible conditions thus represent two ends of a foraging perceptual spectrum.

A new food pellet was dropped in one of two resource pools every  $4/N$  seconds (where  $N$  is the number of participants), and there were three distribution conditions that probabilistically determined which pool received the pellet: 50/50, 65/35, and 80/20. For example, in the 65/35 distribution condition, 65% of food arrived at one pool while 35% arrived at the other pool. At each pool, new pellets were dropped according to a Gaussian distribution with a mean at the pool's center and a variance of 5 units horizontally and vertically. Food release was constrained so that only one pellet could occupy a cell at a given time, and resource pool locations changed from session to session. In the invisible perceptual condition, a pellet appeared on the screen for two seconds for the participant who stepped on it, so participants could gradually ascertain the locations of the resource pools by exploring the world and occasionally obtaining pellets.

Equation 1:

$$Value(i,j) = (P_1 * Distance) + (P_2 * GoalBias) + (P_3 * FoodDensity) - (P_4 * AgentDensity)$$

Equation 2:

$$Probability\ of\ moving\ to\ space(i,j) = \frac{e^{Value(i,j)/K}}{\sum_x \sum_y e^{Value(x,y)/K}}$$

Equation 3:

$$Value(i,j,t) = Value(i,j,t-1) + (P_1 * Reward) + (P_2 * GoalBias) - (P_3 * Penalty) + (P_4 * AgentDensity)$$

**Table 1: Equations**

Goldstone and Ashpole found significant undermatching at the 80/20 and 65/35 distribution levels, with more pronounced undermatching in the more extreme 80/20 conditions. Goldstone et al. (2005) extended the foraging experiment to split perceptual conditions: invisible resources with visible agents, and visible resources with invisible agents. Undermatching was found for the invisible resources/visible agents condition, and the authors conclude that social band-wagoning therefore did not occur, since band-wagoning would lead foragers to overmatch to an 80% pool. The visible resources/invisible agents condition led to the rare phenomenon of overmatching, presumably because participants saw the faster appearance of food at the 80% pool but were not dissuaded by the greater density of foragers at the pool because the foragers were invisible.

### EPICURE: The Full Model

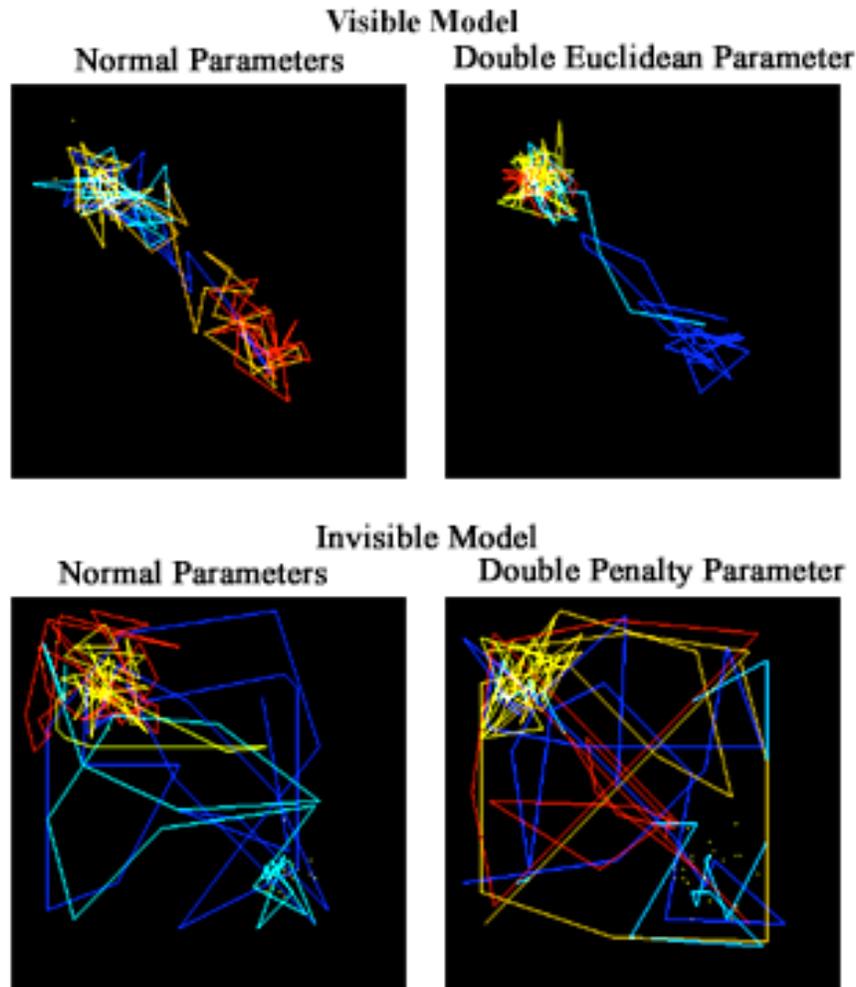
In our agent-based model, EPICURE, each agent is randomly assigned a location on the 80 x 80 grid-world at the beginning of the experiment. As in Goldstone and Ashpole (2004), food is dropped at a rate of 4/N seconds, and unless stated otherwise, N is set to 20 agents, corresponding to the average number of participants in the Goldstone and Ashpole experiment. Agents move every 100 milliseconds, and a movement consists of choosing an available food pellet and moving one grid unit towards the chosen pellet. The sources of agent information vary according to the experimental condition.

During each time step in the visible resources/visible agents condition, each agent judges the value of every available piece of food relative to the agent. Four factors determine a pellet's worth: 1. Euclidean distance from the agent to the pellet, 2. Euclidean distance from the pellet to the agent's sustained goal location, 3. Food density in the local area of the pellet, and 4. Agent density in the local area of the pellet. Each factor is multiplied by a free parameter that reflects the weight of the factor, yielding Equation 1.

The model incorporates softmax action selection in Equation 2 to probabilistically choose a pellet, given each pellet's relative value to the agent calculated in Equation 1. Although we have tried to make the expression generic to

also accommodate the full version of the model, we should point out that the denominator in Equation 2 only sums over pellets currently on the gridworld. With softmax, K is a constant that shifts action selection to be more exploratory or more exploitative of the obtained information. Together, the Euclidean measures and softmax create a degree of agent independence while maintaining the essential dependence on resource and agent distributions for choosing where to move. For the visible resources/invisible agents condition, we set the agent density parameter to 0. Thus, agents move towards food pellets on the basis of distance, food density, and goal bias, but their decisions are not affected by the presence of other invisible agents in the world.

Although we exclude reinforcement histories from these visible resources conditions, the invisible resources conditions require the agents to consider obtained resources information while no longer having information regarding the available resources. In our model, each agent has memory for all cells in the 80 x 80 gridworld. At the beginning of a session, every cell in an agent's memory is initialized to a constant value. Thus, every cell looks equally attractive for action selection purposes. During a time step, each agent chooses a cell by estimating every cell's value (Equation 3) and then using softmax (Equation 2) to assign a movement probability to each cell. If an agent steps on a cell and receives a pellet, the cell's value receives a large boost in the agent's memory, and the neighboring cells are also boosted to a lesser extent. This neighborhood assumption leads to quicker learning, and its ecological validity arises from research on area-restricted search (Croze, 1970; Thomas, 1974). The boosted values increase the probability of choosing those cells in the future. When an agent steps on a cell without receiving a pellet, however, a penalty is assessed to the cell and its neighbors. We set the relative strength of a neighbor's reward or penalty as a linear inverse function of its distance from the current cell. For the invisible resources/visible agents condition, we use the same parameter values, but we also add the agent density factor described in the visible food model. Thus, an agent makes a movement decision based on its history of obtained resources and the current locations of other foragers.

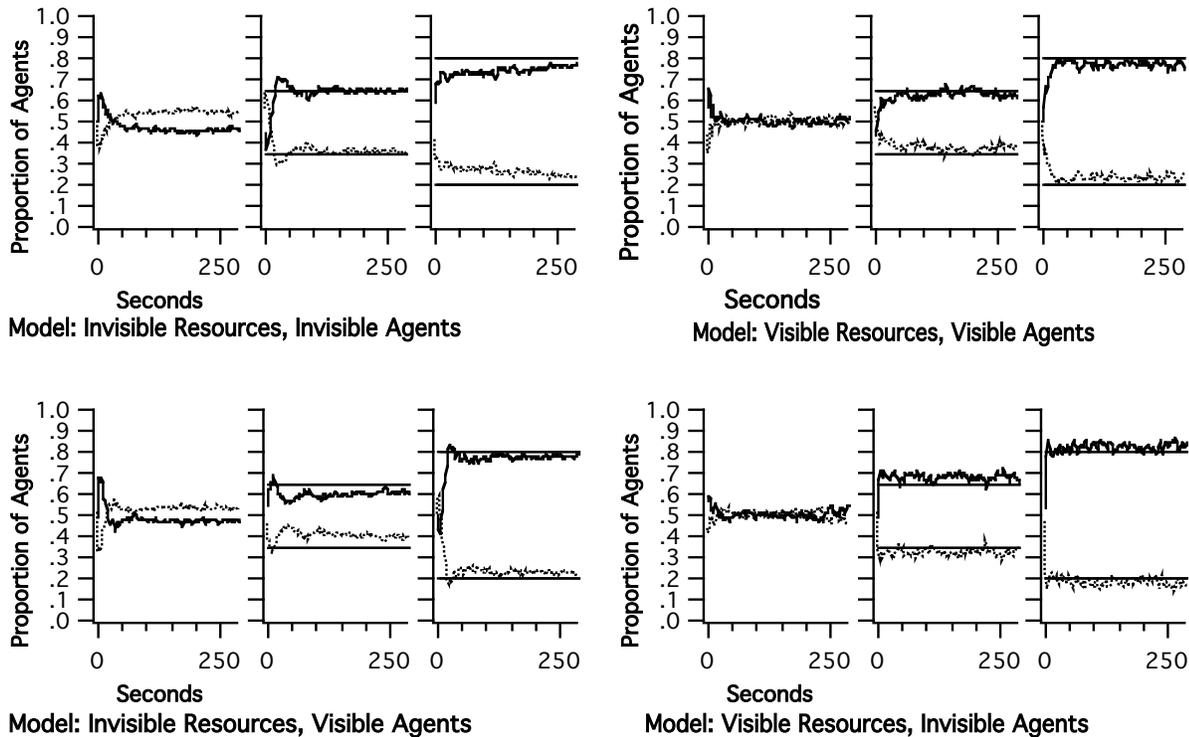


**Figure 1: Movement Profiles**

The full EPICURE model incorporates all of the aforementioned factors: Euclidean distance to visible food pellets, food density, agent density, and goal bias. Furthermore, it integrates this available resources information with the agent's personal history of obtained resources. Although for simplicity we will present our results in terms of the constrained model corresponding to each condition, note that this is equivalent to setting some parameters of the general model to 0.

The balance of parameter weights is critical to the agents' performance. Each picture in Figure 1 shows the color-coded movement history of a typical agent during a five-minute experiment. The gridworld has dimensions of 80x80, and there is an 80% pool in the upper left at coordinates (20, 20) and a 20% pool in the lower right at coordinates (60, 60). In each case, there are actually 20 agents participating, but for ease of understanding, we are showing individual agent results. The left pictures show an agent's behavior using the balanced parameter sets of the respective models, and their movement profiles look very similar to typical profiles of human participants in the Goldstone et al. experiments.

The right pictures show typical agent movements after one parameter has been adjusted in each model. In the visible model, we doubled the weight of the Euclidean distance parameter, and the resulting agent behavior shows much less movement variance. After reaching the 80% pool, the agent essentially stays near the center of the pool, never venturing for food on the periphery, even though the agent may face less competition on the periphery. In the invisible model, we doubled the penalty parameter, and the resulting agent behavior shows much more exploration. Although the reward parameter still has a much higher value than the penalty parameter, the agent now spends less time in a pool if it does not consistently receive rewards. It leaves the 80% pool to further explore the world, but it eventually returns to the pool after penalizing other areas for not containing food. It is worth noting that both of these alternate behaviors are reasonable and even seem to resemble the movement profiles of a few human participants, but our final set of parameters is more representative of the performance of most human participants. The variance in human behavior may be even



**Figure 2: EPICURE matching results**

better modeled by making each agent slightly different by adding Gaussian variance to their parameters, but we want to show that undermatching can arise even when agents are identical.

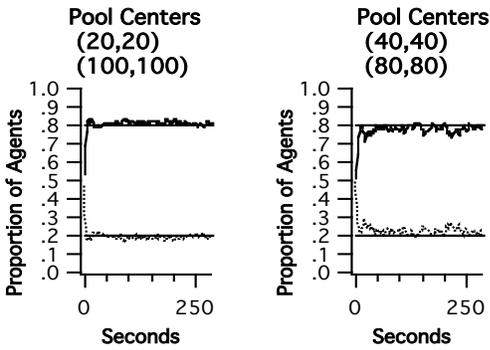
### Undermatching

Figure 2 shows the EPICURE matching results for each information condition. For a given condition, the model uses the same parameter values to simulate foraging behaviors for the 50/50, 65/35, and 80/20 resource distributions. The graphs show the proportion of agents in each pool (within a 25 unit radius of a pool's center, and each center corresponds to its location in the Goldstone et al. conditions) at a given time, after normalizing to exclude agents outside both pools, and each graph shows averaged results from 30 trials, with 20 agents per trial. The matching results capture the undermatching reported by Goldstone and Ashpole (2004), and it also displays the overmatching found in the visible resources/invisible agents condition of Goldstone et al. (2005).

EPICURE indicates the contingent role of agent density. In order to capture the different agent visibility effects from the experiments, the agent density factor in the model is negative for the constrained visible resources model, making an agent less likely to move towards a pellet surrounded by other foragers, but the factor is positive for the constrained invisible resources model, making an agent more likely to choose a cell surrounded by other foragers. Goldstone et al. (2005) hypothesized that social bandwagoning behavior might occur in the invisible

resources/visible agents condition, but they concluded the data did not show evidence of that phenomenon. However, EPICURE indicates that some degree of bandwagoning behavior must occur, since agents are attracted to areas with other agents, and the point gains support from further examination of the empirical data. Bandwagoning occurs early in the trial as individuals make use of the only available information: the locations of other foragers. Later in the trial, behavior becomes dominated by personal reward history rather than the locations of other agents. The condition still results in undermatching because foragers rely on actual rewards rather than a positive feedback cycle of attraction, but they use agent visibility information to find the resource pools more quickly. Our analysis is consistent with claims by Boyd and Richerson (1988) that the relative usage of personal and social information depend on the difficulty and danger of a task. Similarly, Kendall, Coolen, and Laland (2004) found that naïve guppies conformed to prior social information, but experienced guppies made foraging decisions based on their prior experience rather than social information.

Given the apparently robust performance of EPICURE in matching human results, we can now discuss additional simulations designed to discover the source of undermatching. For the following simulations, we focused on comparing the invisible resources/invisible agents ("invisible condition") and visible resources/visible agents ("visible condition") conditions from Goldstone and Ashpole (2004). For each simulation, the parameter values were the same as those used to fit the human data above.



Model: Visible Resources, Visible Agents

Figure 3: Effects of travel costs

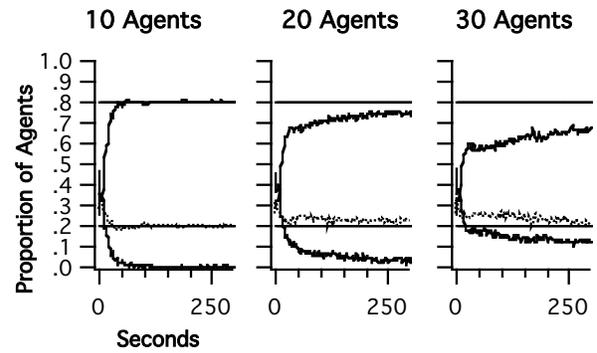
### Travel Costs

Undermatching could arise from the implicit travel cost of switching pools. To test this explanation, we expanded the gridworld to 120 x 120 cells, and we compared simulations with pool centers at (20, 20) and (100, 100) to simulations with pool centers at (40, 40) and (80, 80). Figure 3 shows the simulation results, averaged over 30 trials, for the visible condition. The increased distance between pools leads to nearly perfect matching, which agrees with the empirical pigeon foraging results found by Baum and Kraft (1998). As the distance between pools increased, the pigeons more closely matched the IFD, and they switched pools significantly fewer times. Likewise, in our simulation, the far apart pools led to significantly fewer average switches than the closer pools. As the pools become more separated, it is less likely that an agent will probabilistically choose to switch pools, because the other pool's pellets are so far away, leading to small Euclidean components. The decreased switching promotes better matching because the new pool must appear to be consistently better in order for the agent to complete the journey. The invisible condition shows similar levels of undermatching regardless of the distance between pools. In that condition, the agents continually explore the world and only settle in consistently rewarding locations. Even then, the agents will leave the area if they cease obtaining rewards.

### Number of Agents

Travel costs affect the matching results for the visible condition, but the lack of changes for the invisible condition leads us to believe that another factor contributes to undermatching. We examined the effects of different numbers of foragers by running visible and invisible condition simulations at the 80/20 distribution level with 10, 20, and 30 agents, respectively. Agents began in random locations in an 80 x 80 gridworld with pool centers at (20, 20) and (60, 60). Unlike previous simulations, the food rate was held constant across conditions, with food dropped every 4/20 seconds (200 milliseconds).

Figure 4 shows the non-normalized matching results (the bottom line indicates the proportion of agents outside both

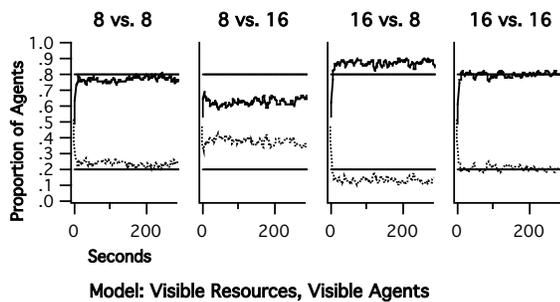


Model: Invisible Resources, Invisible Agents

Figure 4: Effects of the number of agents

pools), averaged over 30 trials, for 10, 20, and 30 agents in the invisible condition. Both the visible and invisible conditions are susceptible to greater undermatching as more agents compete for the food, but there are key differences. The visible condition displays undermatching even when the food rate is doubled, with 10 agents competing for the number of pellets previously given to 20 agents. In essentially a visible resources/visible agents condition, Baum and Kraft (1998) found that pigeons continued undermatching as the food rate increased, so they concluded that food rate did not affect undermatching, but we contend below that the food rate was not high enough to change the task demands. In contrast, EPICURE shows that the invisible condition matches perfectly when 10 agents receive more food, and an increase in the number of agents has greater effects on matching proportions than in the visible condition.

Our novel explanation for undermatching contends that the spatial environment of foraging critically determines how well foragers can distribute to the resources. In the context of the Goldstone and Ashpole (2004) visible condition, a relatively small number of foragers can cover the two resource pools and easily pick up food soon after it is dropped every  $4/N$  seconds, because the food rate is not high enough to tax their foraging abilities. The Gaussian food distribution enhances this effect, because only a few foragers are needed to pick up the majority of the food near the Gaussian centers, while a few additional foragers can dart to the food dropped on the peripheries. By this argument, the available resources decrease the largest amount with the addition of the first few foragers, so there is a smaller marginal gain if more foragers are added. The notion is that every agent can "patrol" a particular area with an efficiency that is relatively, though not completely, independent of the number of resources dropped in their patrolled area. Baum and Kraft (1998) supports our spatial explanation. When the two resource pools were feeding bowls, the pigeons showed significantly greater undermatching than when the resource pools were larger feeding areas or elongated troughs, which we claim provide more information to the average forager because they cannot be exploited as easily by a few foragers.



**Figure 5: Effects of uniform variance**

### Uniform Variance

In the Goldstone and Ashpole (2004) and Goldstone et al. (2005) experiments, both resource pools have equal variances, and so can support agents in numbers that are more similar than predicted by the pools' productivities. These considerations seem to be absent from the literature, and that may be due to the preponderance of models that treat foraging and probability matching as discrete choices between options (Harley, 1982; Regelman, 1984; Bernstein et al., 1988; Seth, 2002), rather than often occurring in spatially instantiated situations.

We should expect significantly less undermatching if our experimental paradigm used uniform variance food distributions rather than Gaussian distributions, because the Gaussian distribution allows a lucky few foragers to collect most of the food at the center, greatly decreasing the distinguishing information between pools and requiring fewer foragers. Figure 5 shows results for visible condition simulations using uniform variance distributions. The first number in each graph indicates the radius (for simplification, a centered square was used) of food droppings in the 80% pool, and the second number indicates the radius of food droppings for the 20% pool. Thus, the "16 vs. 8" condition creates an 80% pool that is four times larger than the 20% pool (1024 cells compared to 256 cells), so the probabilistic food distribution is reflected by pool size.

The graphs clearly support our undermatching explanation. When the pool variances are identical (8 vs. 8), the agents slightly undermatch to the resources. In the 8 vs. 16 condition, dramatic undermatching occurs because it takes more agents in the 20% pool to cover the much larger area. The pick-up time in the 20% pool increases as agents converge, then new pellets dropped far away from the group attract additional foragers to switch from the 80% pool. In the 16 vs. 8 condition, the rarely observed phenomenon of overmatching occurs, and the explanation lies in the fact that the *densities* of the pools are equal, but the *coverage times* are unequal because the food rate is low. As each new piece of food is grabbed relatively quickly, foragers begin to converge as they chase new pellets. This convergence, along with the large pool size, gradually increases the time it takes to reach a new pellet on a far side of the pool, and therefore the new pellet looks more attractive to migrators switching pools. Meanwhile,

agents in the 20% pool have less area to cover and fewer pieces of food, so the pick-up time remains comparatively low. Finally, in the 16 vs. 16 condition, nearly perfect matching is observed. In this case, food rate is the only factor that distinguishes between the two pools. Our simulations reproduced the qualitative results from Baum and Kraft (1998) with 8 vs. 8 as the bowl condition, and 16 vs. 16 as the trough condition. Our invisible condition graphs show a different pattern but also support our explanation: undermatching increases as the 80% pool size decreases.

### Wealth Distribution

An examination of the wealth distributions from Goldstone and Ashpole (2004) indicates that the invisible condition had a significantly greater wealth disparity than the visible condition. This finding is consistent with our interpretation that a lucky few foragers quickly find the pool centers in the invisible condition and remain there, making it very difficult for latecomers to discover the pools. Similarly, Gillis and Kramer (1987) found significantly greater undermatching in 240 zebrafish than 30 zebrafish despite an identical food rate per fish and a decrease in shows of aggression as forager density increased. We contend that the greater prey density allowed some individuals to fare particularly well in the pool centers and decrease the information for everyone else, yet the decrease in aggression indicates that interaction history, rather than competitive ability, may have created the disparities.

Table 2 shows the Gini coefficients for the 80/20 distribution conditions of the Goldstone and Ashpole (2004), Goldstone et al. (2005), and EPICURE results. Gini coefficients range from 0 to 1, and a higher coefficient indicates greater wealth disparities, i.e. some foragers are disproportionately more successful than others. It may appear surprising that the empirical visible condition trends towards greater wealth disparity than the empirical invisible condition, although the trend is not significant. It is worth noting that the invisible condition showed a particularly large standard deviation, and the largest group of participants (28) also showed the largest Gini coefficient (.27). However, the empirical comparisons are difficult due to the relatively small number of groups (8 for Goldstone and Ashpole, 2004; 10 for Goldstone et al., 2005) and the large standard deviations.

EPICURE wealth comparisons are much easier to make because we simulated 30 trials per condition. As our explanation predicts, both invisible resources conditions show significantly greater wealth disparities than their visible resources counterparts. Our agent-based model lacks trait differences among foragers, so the 'good' competitors in the invisible resources conditions are those who happen to find the pool centers early in the experiment, and their early success leads them to stay near the high reward centers. The 'poor' competitors are those who arrive a bit later and receive less information because the early foragers exploit the pool centers. A forager's success can be largely determined by its early interaction

| Condition   | Mean | S.D. | Significant<br>$p < .05$ |
|---|------|------|--------------------------|
| Empirical<br>Invisible Resources,<br>Invisible Agents | .139 | .097 | No                       |
| Empirical<br>Visible Resources,<br>Visible Agents     | .198 | .040 |                          |
| Empirical<br>Invisible Resources,<br>Visible Agents   | .097 | .063 | No                       |
| Empirical<br>Visible Resources,<br>Invisible Agents   | .110 | .047 |                          |
| EPICURE<br>Invisible Resources,<br>Invisible Agents   | .151 | .023 | Yes                      |
| EPICURE<br>Visible Resources,<br>Visible Agents       | .102 | .014 |                          |
| EPICURE<br>Invisible Resources,<br>Visible Agents     | .156 | .017 | Yes                      |
| EPICURE<br>Visible Resources,<br>Invisible Agents     | .101 | .030 |                          |

**Table 2: Gini coefficients**

history, and in a group foraging situation, each forager's relative success can get locked-in for the long term due to interdependencies.

## Conclusions

We have proposed an agent-based model, EPICURE, that captures important empirical results from animal and human group foraging tasks. EPICURE demonstrates that spatial food distribution, food rate, and foraging group size can interact and cause undermatching. These effects are more pronounced for the invisible resources conditions, where an agent's explorations are greatly affected by the success of other agents. Furthermore, EPICURE indicates that a limited degree of social band-wagoning can occur in human foraging when individuals rely on social information prior to establishing personal information.

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