

# EPICURE: Spatial and Knowledge Limitations in Group Foraging

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We propose an agent-based model of group foraging, EPICURE, for patchily distributed resources. Each agent makes probabilistic movement decisions in a gridworld through a linear combination of current perceptual information and a reinforcement history. EPICURE captures the empirical results from several foraging conditions in previous works, and it leads to a reevaluation of findings from those papers. In particular, human foragers show contingent usage of information, initially using social information to discover resource pools before private sampling information has been established. We describe a series of simulations that test the sources of resource undermatching often found in group foraging experiments. After testing the effects of foragers' starting locations, travel costs, the number of foragers, and the size of uniform food distributions, we discuss a novel hypothesis for undermatching. Spatial constraints lead to inadequate individual and group information sampling and cause group undermatching. The foraging group size, food rate, spatial distribution of food, and resulting forager reinforcement histories interact to produce undermatching, and occasionally overmatching, to resources.

**Keywords** agent-based models · foraging · resource allocation · group behavior · social information · undermatching

## 1 Introduction

Animals often forage for resources and even mates in groups. Concrete foraging tasks include chimpanzees foraging for fruit (Hashimoto et al., 2003), ladybird beetles foraging for aphids (Kareiva & Odell, 1987), and guppies choosing mates (Dugatkin, 1992). Meanwhile, abstract foraging tasks include pigeon problem-solving (Giraldeau & Lefebvre, 1986), human information foraging (Pirolli & Card, 1999), and Internet dating sites. 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. There is an interesting interplay between each individual's strategy and the emergent group behavior, which is often not representative of any of its constituents' behaviors (Baum & Kraft, 1998). In this article, we offer a link between individuals' foraging decisions and group foraging distributions.

The ideal free distribution (IFD) model (Fretwell & Lucas, 1970) predicts that a group of foragers will distribute themselves to resource patches in proportion to the relative resources available at each patch. In an

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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. In predicting this optimal distribution, the model assumes the foragers have both freedom of movement and “perfect knowledge” of the locations, amounts, and appearance rates of all the resources, thereby allowing the foragers to correctly assess the value of the resources and optimally distribute as a group. However, in experiments with two patch options, many studies report systematic undermatching in which fewer foragers than expected attend the more profitable patch while more foragers than expected attend the less profitable patch. Godin and Keenleyside (1984) found undermatching in cichlid fish, with the largest degree of undermatching occurring in the condition with the largest rate difference between resource pools. Gillis and Kramer (1987) obtained similar results for large populations (120 and 240) of zebrafish distributing between three resource pools, although they did not find significant deviations for small populations (30 and 60).

Whereas Godin and Keenleyside concluded that differential competitive abilities had violated the IFD assumption of equal payoff for each animal at a pool, Gillis and Kramer concluded that high population density broke the IFD assumption of perfect information. Despite the difference in emphasis, both studies seem to agree that perceptual limitations—whether due to individual ability or occlusion from high density—led to decreased available information about the pools and subsequently undermatching. However, other studies (Harper, 1982; Kennedy & Gray, 1993) cite competitive differences between organisms and travel costs between locations as critical factors in producing undermatching. Baum and Kraft (1998) consistently found undermatching in a group of 30 pigeons distributing between two resource patches, although the degree of undermatching varied as a factor of resource distributions and travel constraints, and they were unable to detect whether competitive abilities varied. However, undermatching continued even as the food rate increased, so Baum and Kraft concluded that food rate did not affect undermatching. 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” (Kennedy & Gray, 1993, p. 165) may all lead to undermatching and violate the IFD.

As Pirolli and Card (1999) have demonstrated, the study of foraging is important for cognitive science because humans may use the same mechanisms in their distribution to information resources and physical resources. In fact, dopaminergic activity appears to critically determine the degree of area-restricted search in food foraging as well as the degree of goal-directed cognition in humans (Hills, 2006). Recently, Goldstone and Ashpole (2004) and Goldstone, Ashpole, and Roberts (2005) examined human group foraging behavior under several perceptual conditions. The two papers present results for all four permutations of visible/invisible resources and visible/invisible foragers, with foragers competing online for resources in an  $80 \times 80$  gridworld with 50/50, 65/35, and 80/20 food distributions at two resource pools. We briefly review the experimental setup and results from these articles, and then describe an agent-based model that provides candidate mechanistic explanations for group foraging dynamics. The model allows us to test changes in dynamic group behavior as a result of environmental manipulations, and it gives rise to a novel explanation of resource undermatching in group foraging.

Traditional close-formed equation foraging models suffer from limitations similar to the mean field approximation, according to which all individuals in a group are assumed to be in the same location and experience the same local environment. Agent-based models that incorporate space and local variability frequently produce much more realistic models (Seth, 2001). For example, giving agents unique rather than aggregate positions has proven invaluable in modeling the continued stability of host–pathogen populations (de Aguiar, Rauch, & Bar-Yam, 2004), the genetic diversity in a population (Rauch & Bar-Yam, 2004), and preserved pockets of cooperation surrounded by defectors (Fehr & Fischbacher, 2004; Nowak & May, 1992). We contend that Kennedy and Gray’s (1993) meta-analysis undoubtedly describes many important factors in undermatching to resources, but as a result of past models driving the empirical observations, spatial constraints and their implications for resource undermatching have been overlooked in previous studies.

## 2 Human Group Foraging

Goldstone and Ashpole (2004) recently examined dynamic group foraging behavior in humans by developing an experimental networked Java platform to create a common two-dimensional virtual world (an  $80 \times 80$  grid) shared across computers. Participants sat at their respective computers and foraged for resources in real time, 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 the Goldstone and Ashpole foraging environment and data serve as the initial basis for our subsequent agent models.

### 2.1 Methods

In the Goldstone and Ashpole foraging experiments, participants engaged in six 5-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 & 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 is an elegant experimental manipulation because the dynamic group behavior still affects how much food has been eaten and therefore the likelihood that a participant will encounter food. The invisible condition corresponds to foraging experiments with sampling under uncertainty, i.e. only probabilistic information is available. The visible and invisible conditions represent two ends of a foraging perceptual spectrum described by Clark and Mangel (1984), although their resulting model dealt with information sharing among foragers.

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 standard deviation 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, and therefore, participants could gradually ascertain the locations of the resource pools by exploring the world and occasionally obtaining pellets.

### 2.2 Results

Goldstone and Ashpole discuss three results: undermatching, systematic cycles of population migration between pools, and high variance of participants' locations relative to food locations. Although our agent-based model captures all of these phenomena using the same parameter values, we are most concerned with explaining the resource undermatching. 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. Since individuals do not directly interfere with each other (two participants can occupy the same location), competitive interference can be removed as a possible explanation of the phenomenon. Furthermore, since undermatching occurs even in the visible conditions, where "perfect" knowledge is available, straightforward accounts in terms of perceptual constraints can be removed as explanations. Our agent-based foraging model, EPICURE (simply a name, not an acronym), seeks to reproduce these results while testing the other undermatching alternatives—different competitive abilities, travel costs, and the number of foragers—from Kennedy and Gray's (1993) meta-analysis.

Goldstone, Ashpole, and Roberts (2005) extended the foraging experiment to split perceptual conditions: invisible resources with visible agents, and visible resources with invisible agents. The latter condition is probably less common in nature, but the invisible resources/visible agents condition is common and serves as an impetus for social learning in many species, from birds to humans, where an individual's resource discovery can refine the searching of fellow foragers. Although no direct communication occurred in our

experiments, this condition could emphasize indirect communication insofar as a forager may infer the location of the invisible food based on the locations of visible agents. Consistent with this hypothesis, field experiments on migratory birds have shown that the presence of birds attracts other birds to the region (Pöysä, Elmerberg, Sjöberg, & Nummi, 1998; Stamps, 1988). Adding birds to a site makes it more likely that still more birds will choose the site for nesting. Another familiar example is the tendency of buzzards to use the presence of other buzzards as an indicator of possible food sources, and therefore to fly to where a large group of buzzards is.

Undermatching was once again demonstrated for this invisible resources/visible agents condition, and the authors conclude that social bandwagoning therefore did not occur, since bandwagoning would lead foragers to overmatch. The visible resources/invisible agents condition led to the rare phenomenon of overmatching, presumably because participants saw the faster appearance of food at an 80% pool but were not dissuaded by the greater density of foragers at the pool because the foragers were invisible.

Undoubtedly the Goldstone et al. foraging paradigm is simplistic compared with natural foraging situations, which include issues of diet selection, territoriality, energy requirements, communication, reproduction, etc. However, the paradigm allows us to take important steps in understanding the effects of the amount and types of information on dynamic group behavior. Human resource undermatching has been demonstrated in an even more abstract design (Critchfield & Attebery, 2003; Sokolowski, Tonneau, & Freixa-Baque, 1999), with 15 participants each choosing to display a green or red sign and contributing a token for each trial, and the experimenters drawing 10 winning tokens according to green pool and red pool payout distributions that varied across games. Similar undermatching results were found when a certain number of points were allocated to each chip color, and the points were equally divided among all members who chose that chip color (Kraft & Baum, 2001). Sokolowski and Tonneau (2004) recently extended their paradigm to three pools, and they again found consistent undermatching with respect to the most profitable resource pool. Furthermore, undermatching results have been obtained with this paradigm even when participants could see each others' pool choices and switch pools before the experimenter

announced results (Madden, Peden, & Yamaguchi, 2002).

### 3 An Agent-Based Model of Resource Matching

In EPICURE, each agent is randomly assigned a location in the  $80 \times 80$  gridworld 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 interesting aspects of the model lie in the parameters for action selection, and the usefulness of each parameter critically depends on the perceptual condition we are modeling. We first describe the full EPICURE model, and then describe how we set certain parameters to zero in order to capture the specific conditions from Goldstone and Ashpole (2004) and Goldstone et al. (2005). An interactive Java version of the model is available at <http://cognitn.psych.indiana.edu/Epicure.html>. We have previously described a less developed version of the model (Roberts & Goldstone, 2005), but here we also include modeling results for Goldstone et al. (2005), a comprehensive examination of our undermatching explanation, and our results on the contingent usage of public and private information.

#### 3.1 Full Model

An agent-based model should have minimal representational requirements while also being sufficiently robust to handle changes in the empirical environment, such as a sudden increase in food rates or number of participants. When the food is visible, foragers are likely to move towards the closest pellet, but this tendency is modulated by the food density around a pellet and the density of competitors around the pellet. Furthermore, each location in the gridworld has a reinforcement history, so foragers are likely to move towards spots that have been profitable in the past, and away from spots where little food has been found in the past. Finally, each of our foragers has a bias to continue moving towards a chosen location until it is reached, before choosing a new location.

Together, these considerations lead to six factors that let an agent determine each location's current worth in the full model:

- (1) Inverse Euclidean distance from the agent to a pellet.
- (2) Food density around a location.
- (3) Agent density around a location.
- (4) Past rewards for finding food at the location.
- (5) Past penalties for not finding food at the location.
- (6) Inverse Euclidean distance from the location to the agent's current goal location.

Each factor is multiplied by a free parameter that reflects the weight given to the factor, yielding Equation 1. Equation 1 indicates that the value of cell  $i, j$  at time  $t$  is the sum of these weighted factors. Note that agent density can be a positive or negative factor, depending on the environmental context, and this will be described further in Section 4.3.

$$\begin{aligned}
 \text{Value}(i, j, t) = & \left( P_1 * \frac{1}{\text{fooddistance}} \right) \\
 & + (P_2 * \text{fooddensity}) \pm (P_3 * \text{agentdensity}) \\
 & + (P_4 * \text{rewards}) - (P_5 * \text{penalties}) \\
 & + \left( P_6 * \frac{1}{\text{goaldistance}} \right)
 \end{aligned} \quad (1)$$

$$\begin{aligned}
 \text{Probability of moving to space}(i, j) \\
 = \frac{e^{\text{Value}(i, j, t)/K}}{\sum_x \sum_y e^{\text{Value}(i, j, t)/K}}
 \end{aligned} \quad (2)$$

The model also incorporates Luce's choice rule (Luce, 1959) in Equation 2 to probabilistically choose a location, given each location's relative value to the agent calculated in Equation 1. With Luce's choice rule,  $K$  is a constant that shifts action selection to be either more exploratory or more exploitative of information already obtained. When  $K$  is large, even highly valued locations become small values and thereby indistinguishable, leading to uniform random movement choices. When  $K$  is small, differences between the location values are exaggerated by exponentiation, and the probability of choosing the highest valued location approaches 1 as  $K$  approaches 0. Accordingly, the behavior of the model becomes more deterministic as  $K$  converges on

0. Together, the location factors and Luce's choice rule create a degree of agent independence while maintaining the essential dependence on resource and agent distributions for choosing where to move. Each agent chooses a respective goal location, and at every time step, each agent either takes a step towards its goal or probabilistically chooses a new goal location.

### 3.2 Constrained Visible Food Model

The visible resources conditions from Goldstone and Ashpole (2004) and Goldstone et al. (2005) could certainly incorporate all of the factors above, but we chose to model the empirical data with a more constrained set of parameters that excluded information on reinforcement histories. Instead, agents in our constrained visible model only use information on the available resources and densities of other agents. The parameters for past rewards and past penalties are set to zero, and agents only choose between pellets that are currently in the gridworld, rather than choosing between all locations in the gridworld. This captures the visible resources/visible agents condition, and for the visible resources/invisible agents split condition, we also set the agent density parameter to zero.

### 3.3 Constrained Invisible Food Model

The invisible resources conditions from Goldstone and Ashpole (2004) and Goldstone et al. (2005) require the agents to consider obtained resources information while no longer having information regarding the available resources. For these conditions, the food distance and food density parameters are set to zero (and for the invisible agents condition, agent density is also set to zero), and agents must rely on their reinforcement histories. Experiments have shown that foragers use memory to return to profitable patches within trials and even across trials (Bell & Baum, 2002; Milinski, 1987; Zach & Falls, 1976). At the beginning of a session, every cell in an agent's memory is initialized to a constant value. 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. 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.

The neighborhood assumption leads to quicker learning, and its ecological validity arises from research on area-restricted search (Bond & Kamil, 2002; Croze, 1970; Hills, 2006; Thomas, 1974) and two cognitive phenomena: perceptual discrimination and generalization. On one hand, human foragers may not be making fine perceptual discriminations between cells, especially given the large number of cells. Thus, a forager may be rewarded at a location but not make a clear distinction between the rewarding cell and the rewarding cell's neighbors. Generalization, on the other hand, implies a more purposeful credit attribution to similar options. If one cell provides a reward, its neighbors may be likely to provide rewards too, because there is often underlying order in the environment, and in the experiments (Goldstone & Ashpole, 2004; Goldstone et al., 2005), participants were explicitly told that the resources occur in clumps. In any case, the boosted values in an agent's memory increase the probability of choosing those cells in the future.

By exploring the environment and obtaining a history of rewards and penalties, each agent constructs a dynamic representation of the resource patches in the environment. This captures the information available in the invisible resources/invisible agents condition, and for the invisible resources/visible agents split condition, we no longer set the agent density parameter to zero.

## 4 Model Results for the Empirical Data

Our goals with EPICURE were to model the empirical data from Goldstone and Ashpole (2004) and Goldstone et al. (2005), and then test the model in alternative conditions, in order to determine the sources of undermatching in the human data.

### 4.1 Undermatching

Figures 1–4 show the human data and model matching results for each information condition. The top of each figure shows the empirical matching results at the three resource distribution levels of Goldstone and Ashpole (2004) and Goldstone et al. (2005), but outliers have been excluded. If a participant was outside both pools for more than 1/3 of the experiment, the participant's data was excluded because it is very unlikely that the individual was following directions. The bottom of each

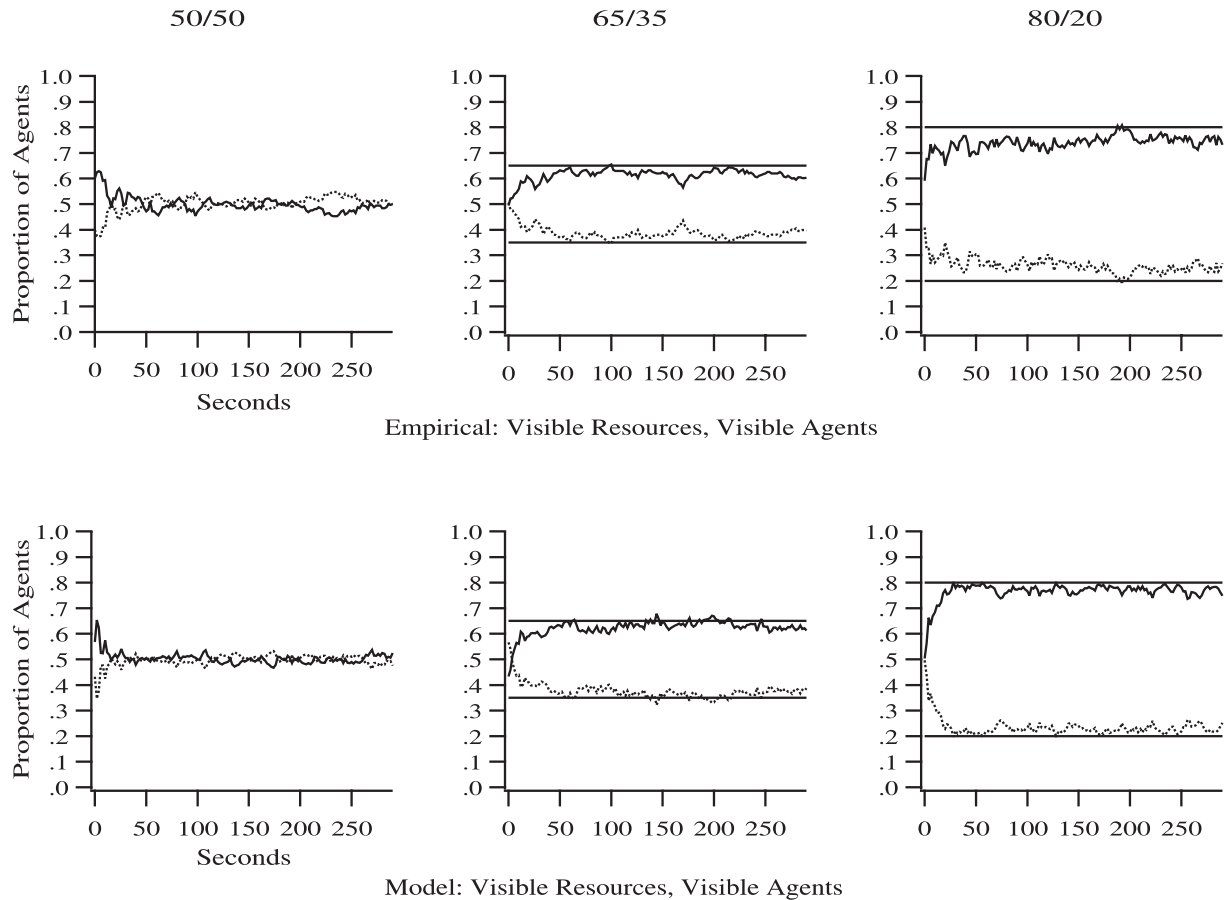
figure shows the model's predictions, and the model uses the same parameter values to simulate foraging behaviors for the 50/50, 65/35, and 80/20 resource distributions. The figure captions include the parameter values for the visible and invisible constrained models. (The parameter weights are different because these are taken from earlier runs of each model, before using the full model equation; however, results are equivalent when using the full model and simply setting the appropriate parameter weights to zero.)

The graphs show the proportion of agents in each pool (within a 25 unit radius of a pool's center) at a given time, after normalizing to exclude agents outside both pools. For the empirical data, the invisible resources/invisible agents and visible resources/visible agents conditions from Goldstone and Ashpole (2004) are averaged from eight groups of approximately 20 participants. The split visibility conditions from Goldstone et al. (2005) are averaged from 10 groups of approximately 28 participants. The model graphs show the averaged results from 30 trials, with 20 agents per trial. EPICURE's results prior to normalization also match Goldstone and Ashpole's results prior to normalization. The matching results show that EPICURE has captured the undermatching reported by Goldstone and Ashpole (2004), and also the overmatching found in the visible resources/invisible agents condition by Goldstone et al. (2005). Overmatching is rare in the foraging literature, and Goldstone et al. attribute their overmatching results to the somewhat unnatural situation where the faster food arrival at one pool attracts a disproportionate number of foragers who are not deterred by invisible competitors.

Equation 3 (Baum, 1974) captures the degree of undermatching or overmatching in a two patch system.

$$\text{Log}\left(\frac{F_A}{F_B}\right) = s\text{Log}\left(\frac{N_A}{N_B}\right) + b \quad (3)$$

The resource amounts in each patch are indicated by  $N_A$  and  $N_B$ , and the numbers of foragers in each patch are  $F_A$  and  $F_B$ . The parameter  $s$  controls the sensitivity of foragers to resource distributions, and  $b$  is a bias parameter. The ideal free distribution model predicts that best-fitting values of  $s$  and  $b$  are 1 and 0 respectively, and undermatching occurs when the value of  $s$  is less than 1. Figures 5 and 6 use this equation to



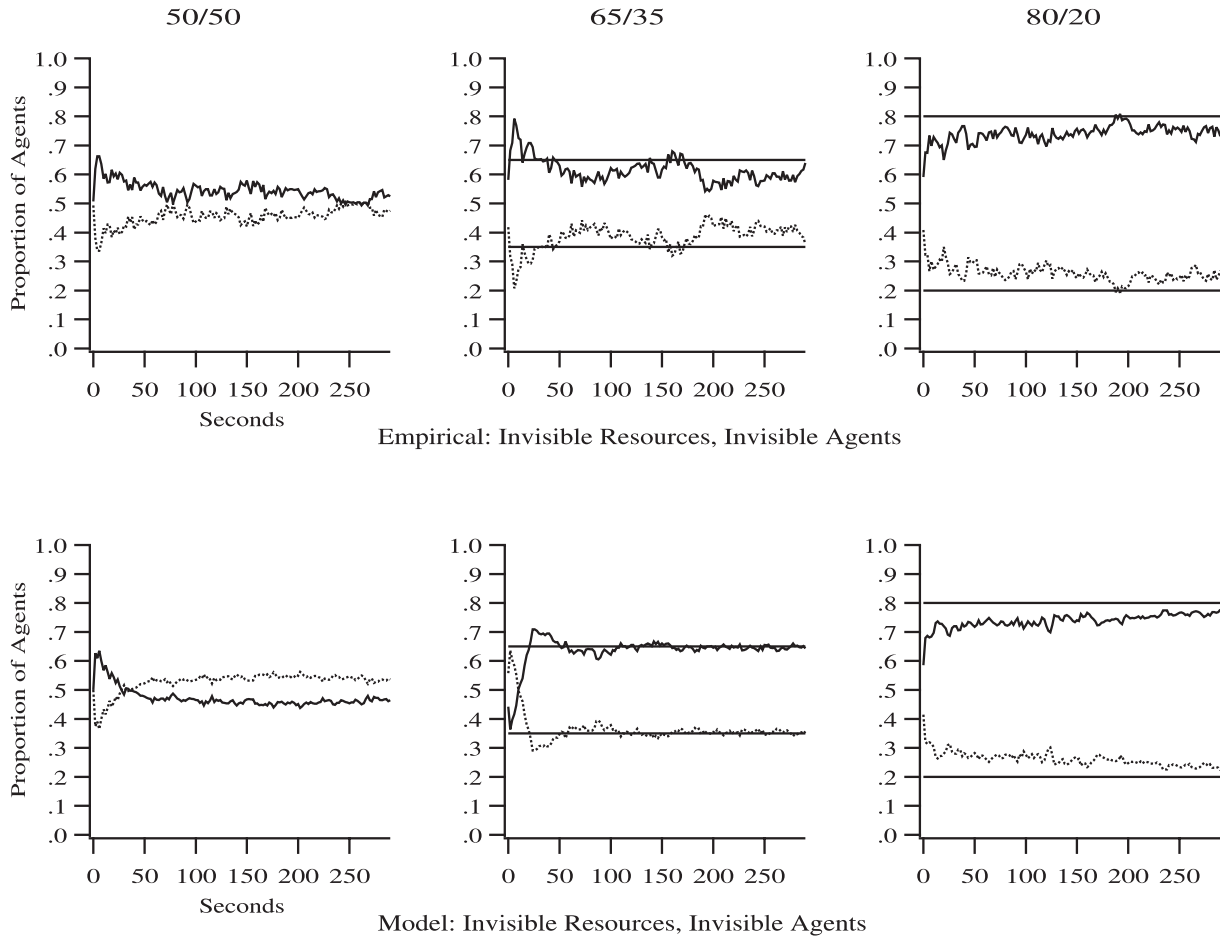
**Figure 1** Empirical and EPICURE matching results for the visible resources, visible agents condition. The top row shows the average matching results from Goldstone and Ashpole (2004) for the 50/50, 65/35, and 80/20 food distribution conditions. The bottom row shows the average of 30 EPICURE trials for each condition, with parameter values: distance = 50.0; goalbias = 10.0; fooddensity = 4.0; agentdensity = 1.0,  $K = 3.0$ .

compare the empirical results and EPICURE predictions.

Table 1 shows a log-likelihood analysis for the invisible resources/invisible agents and visible resources/visible agents conditions. For the former, our full model was the constrained invisible food model described above, and we compared its performance with a restricted model with the goal bias parameter set to zero. Clearly, the full model is significantly better at predicting the observed empirical data. Note that we did not modify the other parameter weights for the restricted model, but in our simulations, no parameter combination can overcome the fundamental problem of this restricted model: Without goal bias, agents hover in the center of the world, briefly moving towards a chosen location on one side before probabilistically choosing a location on

the other side. Similarly, in the visible resources conditions, goal bias prevents agents from switching pools abnormally often.

For the visible resources/visible agents condition, our full model was the constrained visible food model described above, and we compared it with a restricted model with the food density parameter set to zero. This difference between models is also significant, though not nearly as large an effect as for the previous pair. Once again, we did not modify the other parameter weights, and it is possible that an optimal parameter set would show no difference between the models, but we believe food density is important for many general foraging environments. Without food density, agents could not distinguish between pools with large food density differences and equal agent densities.

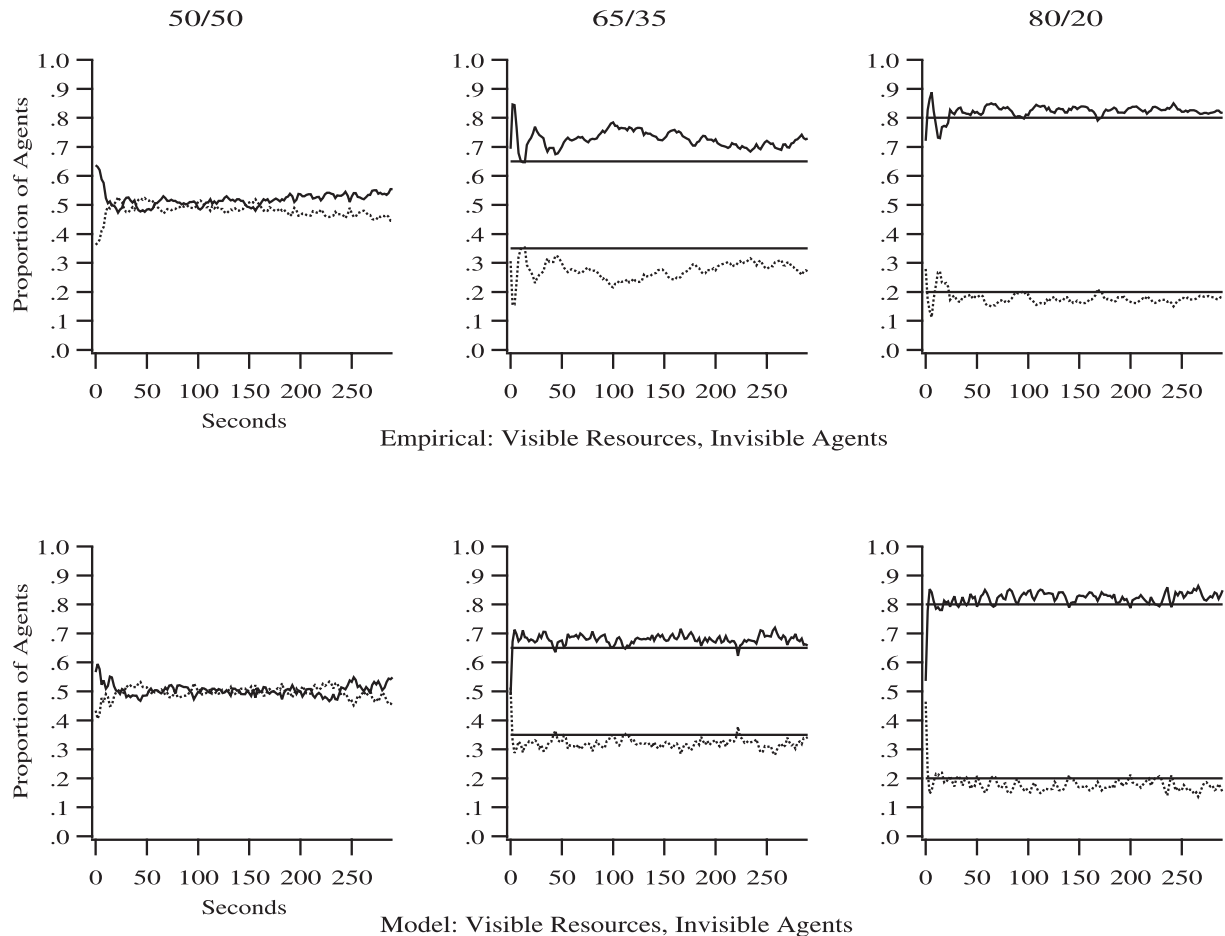


**Figure 2** Empirical and EPICURE matching results for the invisible resources, invisible agents condition. The top row shows the average matching results from Goldstone and Ashpole (2004) for the 50/50, 65/35, and 80/20 food distribution conditions. The bottom row shows the average of 30 EPICURE trials for each condition, with parameter values: reward = 4000.0; goalbias = 3000.0; penalty = 40.0; agentdensity = 0.0, K = 100.0.

**Table 1** Comparison of full and restricted EPICURE models. For the invisible models, we calculated log-likelihood from the empirical data for the full model (the constrained invisible model described in the text) and a restricted model with the goal bias parameter set to zero. For the visible models, we used the constrained visible model described in the text, and a restricted model with the food density parameter set to zero.

	Proportion in 80% pool	$\chi^2$
Empirical invisible	.747	
Full invisible model	.732	$\chi^2(1,30) = 17,129.11$ $p < .01$
Restricted invisible model (no goal bias)	.993	
Empirical visible	.746	
Full visible model	.732	$\chi^2(1,30) = 27.15$ $p < .01$
Restricted visible model (no food density)	.708	





**Figure 3** Empirical and EPICURE matching results for the visible resources, invisible agents condition. The top row shows the average matching results from Goldstone et al. (2005) for the 50/50, 65/35, and 80/20 food distribution conditions. The bottom row shows the average of 30 EPICURE trials for each condition, with parameter values: distance = 50.0; goalbias = 10.0; fooddensity = 4.0; agentdensity = 0.0,  $K = 3.0$ .

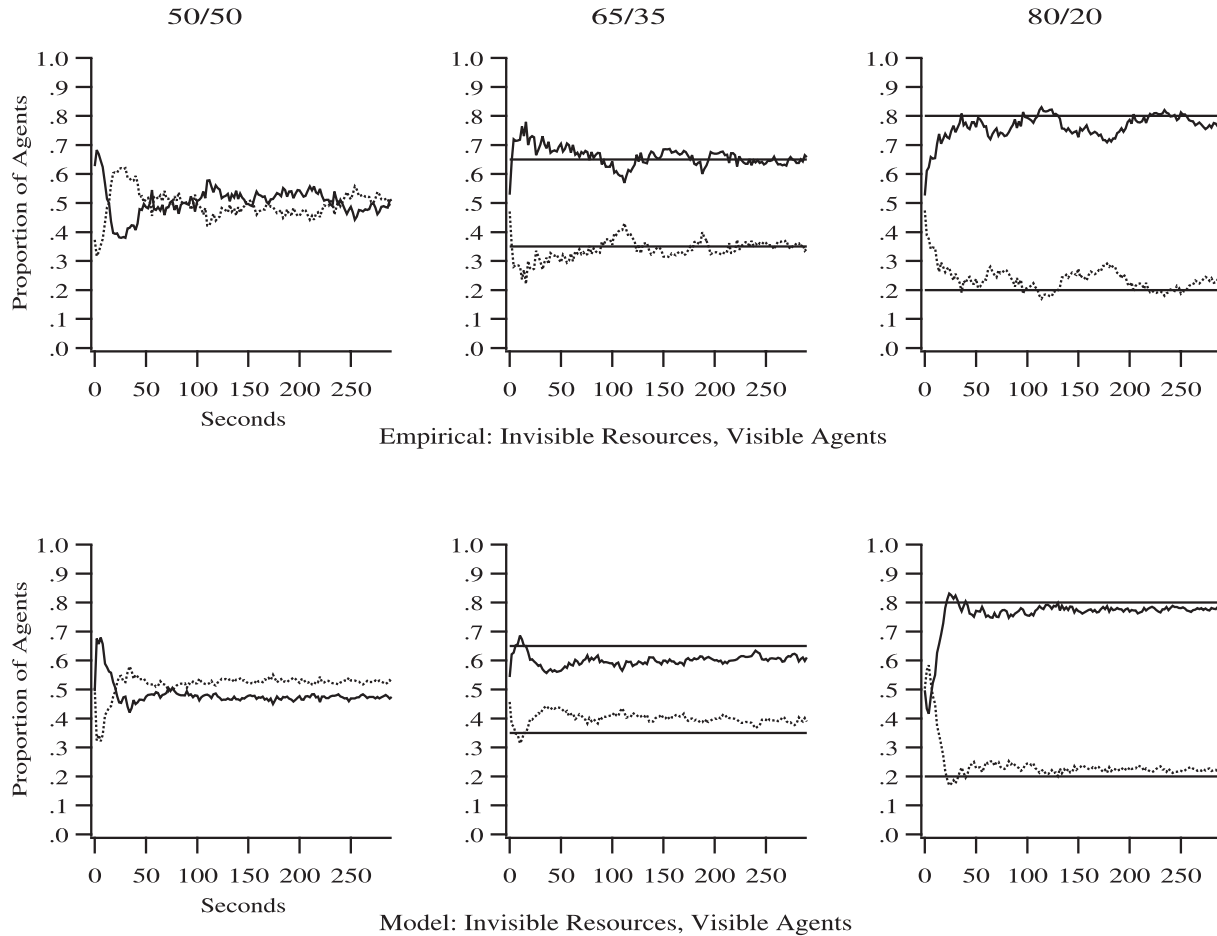
## 4.2 Population Oscillations

EPICURE also exhibited the respective levels of population oscillations found by Goldstone and Ashpole (2004), as well as high variance of agents' locations relative to resource locations and a comparable amount of switching between pools. However, further testing of the model actually led us away from the Fourier analysis because it was shown to be too sensitive to initial conditions. For instance, starting the model's agents at one pool led to large oscillations in the Fourier analysis caused by the early migrations as the foragers exhaust that pool and find the other pool. Furthermore, when we adopted our stricter criteria for excluding outliers in the empirical data, we found that the invisible resources/

invisible agents condition no longer has larger population oscillations than the other empirical conditions. This indicates that the original population oscillation results may have been too sensitive to outlier individuals. Although the analysis may still capture important population trends, we have decided to focus on matching results for the current article.

## 4.3 Variable Role of Agent Density

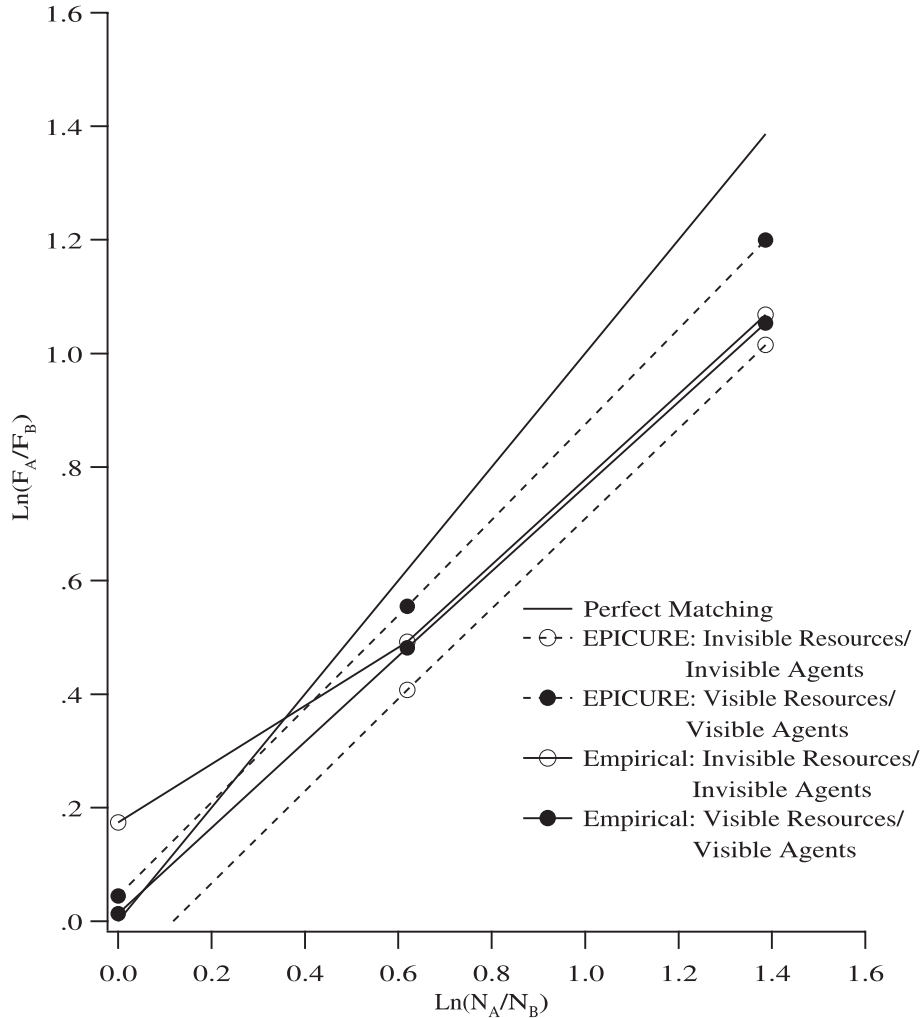
A surprising success of EPICURE is that it shows the contingent role of agent density. In order to capture the different agent visibility effects shown in Figures 5 and 6, the agent density factor in the model is negative for the constrained visible food model, making an agent



**Figure 4** Empirical and EPICURE matching results for the invisible resources, visible agents condition. The top row shows the average matching results from Goldstone et al. (2005) for the 50/50, 65/35, and 80/20 food distribution conditions. The bottom row shows the average of 30 EPICURE trials for each condition, with parameter values: reward = 4000.0; goalbias = 3000.0; penalty = 40.0; agentdensity = 125.0,  $K = 100.0$ .

less likely to move towards a pellet surrounded by other foragers, but the factor is positive for the constrained invisible food model, making an agent more likely to choose a cell surrounded by other foragers. In reevaluating the empirical data (Goldstone et al., 2005), it appears the human foragers tend to find the invisible resource pools faster when the other foragers are visible. We examined the average proportion of foragers in the 80% pool in the first 50 seconds of each invisible resources trial ( $M = 0.549$ ,  $SD = 0.063$  and  $M = 0.52$ ,  $SD = 0.059$  respectively for visible and invisible agents), but the difference was not significant given the small number of trials available for comparison. We found the opposite trend when examining the proportion of foragers outside the pools in the first 50 seconds ( $M =$

$0.242$ ,  $SD = 0.037$  and  $M = 0.271$ ,  $SD = 0.064$ ), although this comparison also did not reach significance. Using our standard of 30 simulations for each condition, the model showed a significantly higher proportion of agents in the 80% pool for the first 50 seconds of the visible agents condition compared with the invisible condition [ $M = 0.579$ ,  $SD = 0.025$  and  $M = 0.543$ ,  $SD = 0.026$ ,  $F(1, 59) = 29.12$ ,  $p < 0.001$ ], and a significantly lower proportion of agents outside the pools for the first 50 seconds of the visible agents condition [ $M = 0.196$ ,  $SD = 0.025$  and  $M = 0.235$ ,  $SD = 0.016$ ,  $F(1, 59) = 49.67$ ,  $p < 0.001$ ]. Bandwagoning seems to occur early in the trial as individuals make use of the only available information: the locations of other foragers. Later in the trial, however, behavior becomes dominated by



**Figure 5** Resource distributions at patches A and B ( $N_A$  and  $N_B$ ) to forager distributions at the patches ( $F_A$  and  $F_B$ ) for the empirical conditions in Goldstone and Ashpole (2004) and the corresponding EPICURE simulations.

personal reward history rather than the locations of other agents.

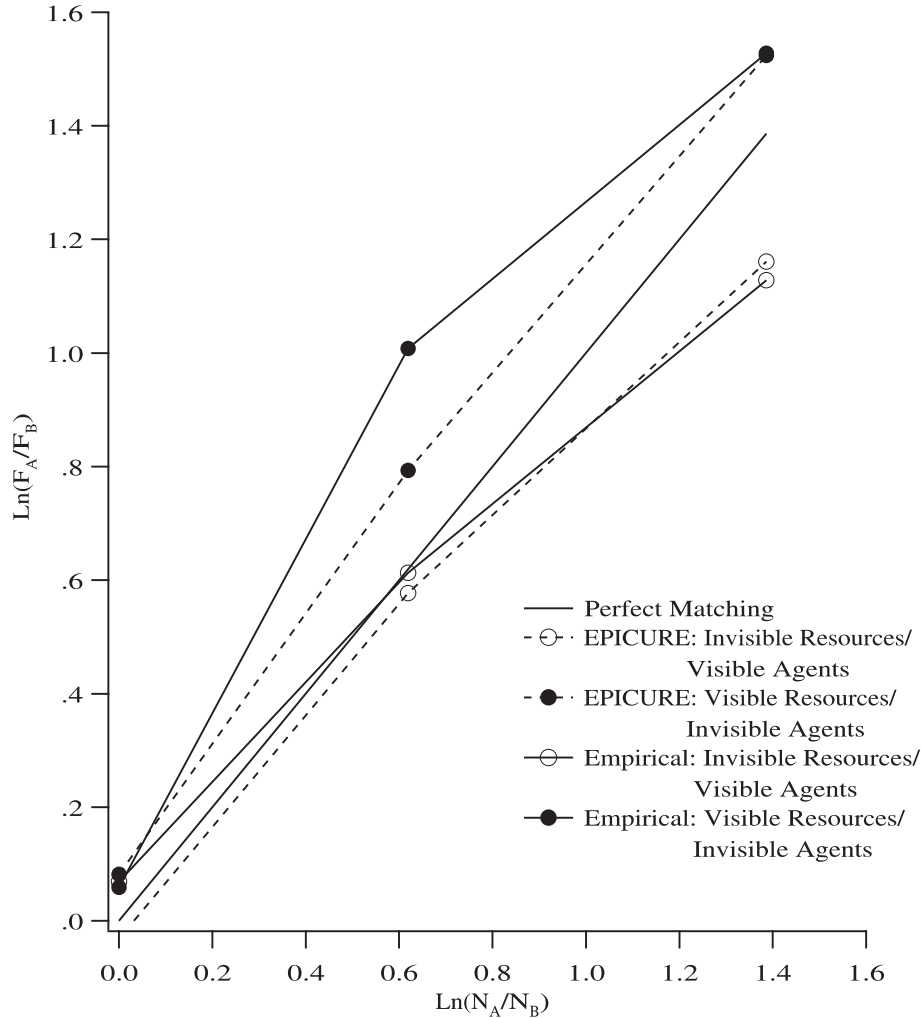
### 5 Additional Simulations to Explain Undermatching

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. Note that given Kennedy and Gray’s (1993) meta-analysis and our earlier analysis of the Goldstone and Ashpole (2004) and Goldstone et al. (2005) results, competitive abilities, travel costs, and the number of foragers could all be causes of undermatching. However, we can eliminate competitive abilities as the explanation here, since the agents in our models all possess the same attributes.

#### 5.1 Starting Locations

Travel costs between resource pools are sometimes used to explain undermatching on the grounds that foragers switch less frequently when the pools are far-

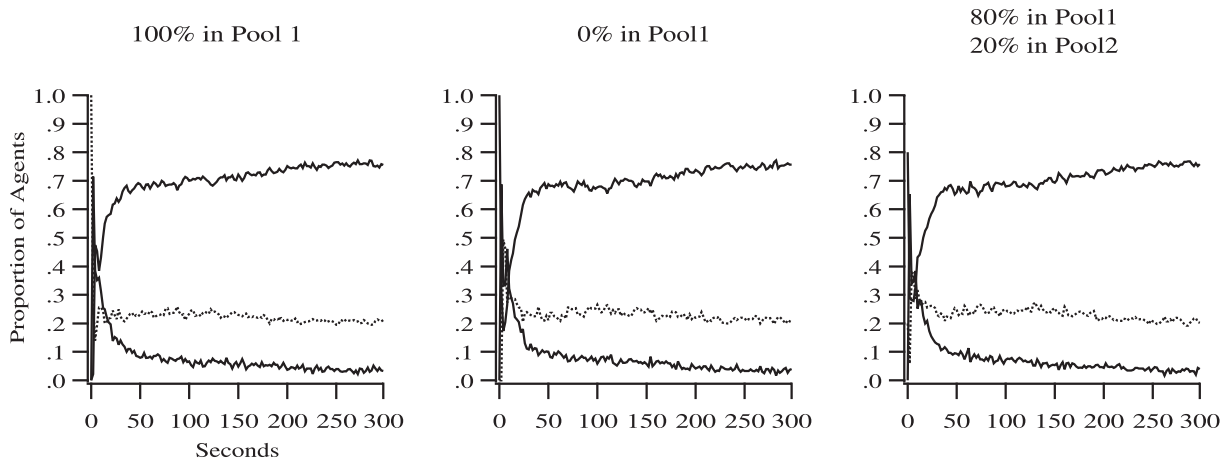


**Figure 6** Resource distributions at patches A and B ( $N_A$  and  $N_B$ ) to forager distributions at the patches ( $F_A$  and  $F_B$ ) for the empirical conditions in Goldstone et al. (2005) and the corresponding EPICURE simulations.

ther apart, and therefore obtain less information about the resources and make worse decisions. In order to test this explanation while trying to avoid possible confounds from changing the world size, we ran two types of simulations. First, we conducted simulations with agents starting inside the pools instead of at random locations around the world.

Figure 7 shows the matching results, averaged over 30 trials, from the invisible condition at the 80/20 distribution level (results were similar for the visible condition and other distribution levels). Here we have included the proportion of agents in neither pool to show that results are identical even before normalization. After normalization, these experiments show less

undermatching than Figure 2, but this is due to a more restrictive definition of being in a pool. For these simulations, we wanted to guard against possible matching biases caused by the pools' respective locations in the gridworld, so we placed the pools in diagonally opposite corners with pool centers at (20, 20) and (60, 60) and restricted the pool definitions (20 units from the center) to avoid intersection with the edges of the gridworld. In the left graph of Figure 7, we started all agents at random locations inside the 80% pool. In the middle graph, we started all agents at random locations inside the 20% pool, and in the right graph, we started 80% of agents inside the 80% resource pool and 20% of agents inside the 20% resource pool.



**Figure 7** EPICURE non-normalized matching results for the invisible resources, invisible agents 80/20 food distribution condition with different agent starting locations. In the left graph, all of the agents start in the 80% pool. In the middle graph, all of the agents start in the 20% pool. In the right graph, 80% of the agents start in the 80% pool and 20% of the agents start in the 20% pool.

All of these experiments result in the same undermatching asymptote despite differences in initial foraging behaviors. In the extreme situations where everyone starts at one pool, the agents quickly exhaust the pool and some find the other pool. Surprisingly, the asymptotic matching remains the same as when agents start in the IFD proportions. Another observation can be made by examining the data prior to normalization. The 20% pool always has approximately 20% of agents, and undermatching seems to arise because some agents leave the 80% pool and are outside both pools. The cost of switching does not seem to drive behavior.

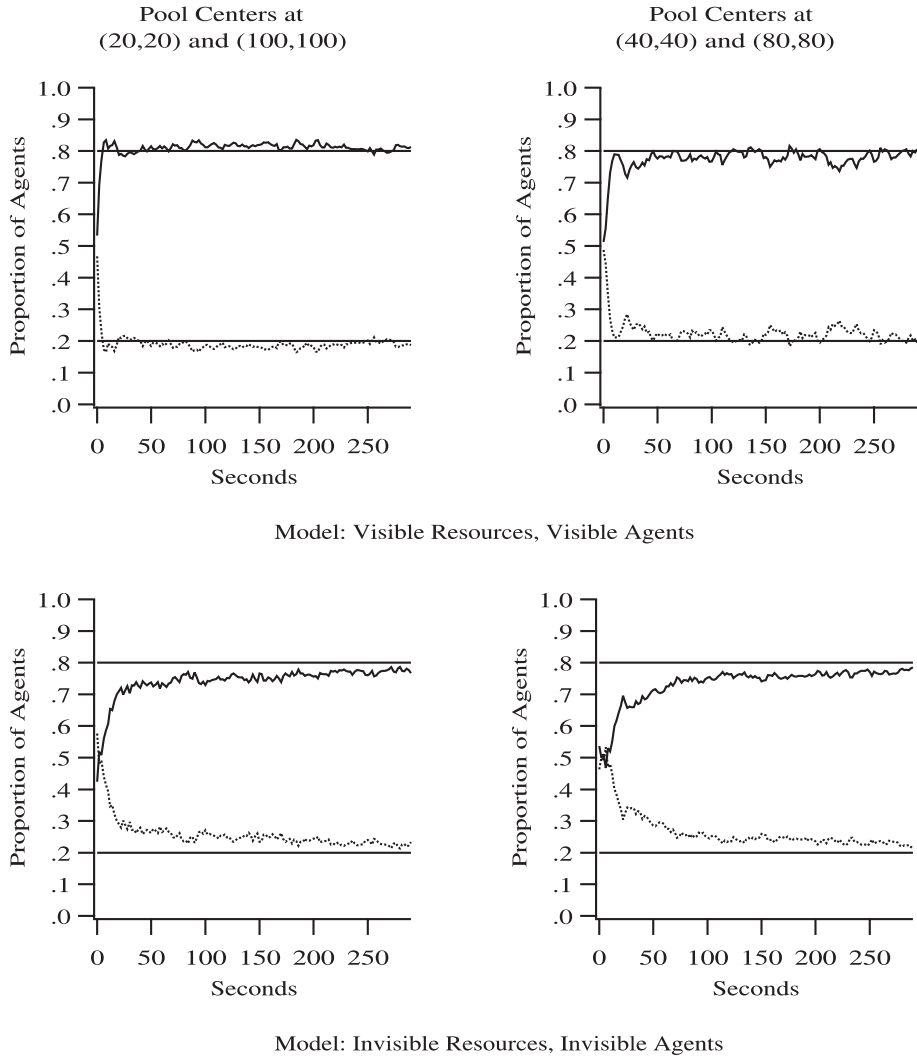
## 5.2 Distance Between Pools

Manipulation of agents' starting locations showed that agents still disperse in the same proportions and therefore undermatching is not caused by a lack of sufficient switching. The other travel cost explanation is that the distance between pools leads to undermatching. To test this explanation, we expanded the gridworld to  $120 \times 120$  cells, and we compared simulations with pool centers at (20, 20) and (100, 100) with simulations with pool centers at (40, 40) and (80, 80). For these simulations, agents started at random locations in the world rather than being concentrated in the pools.

Figure 8 shows that the simulation results differ for the visible and invisible conditions. At the bottom,

the invisible condition shows similar undermatching regardless of the distance between pools. We conclude that the agents using the constrained invisible resources model will continually explore the world and only settle in consistently rewarding locations. Even then, the agents will leave the area if they stop obtaining rewards. In this condition, distance between pools therefore has no effect because the agents will continually explore until they are rewarded again.

In the top part of Figure 8, however, agents in the visible condition are clearly affected by the distance between pools. In fact, the increased distance between pools leads to nearly perfect matching. These results agree with the empirical pigeon foraging results of 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,  $M = 0.146$ ,  $SD = 0.10$  and  $M = 30.72$ ,  $SD = 10.09$ ,  $F(1, 59) = 318.38$ ,  $p < 0.001$ . The dynamics of the constrained visible model offer a simple explanation for these findings. As the pools become more separated, it is much 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. Furthermore, if the agent does decide to switch, the longer distance means there are more oppor-

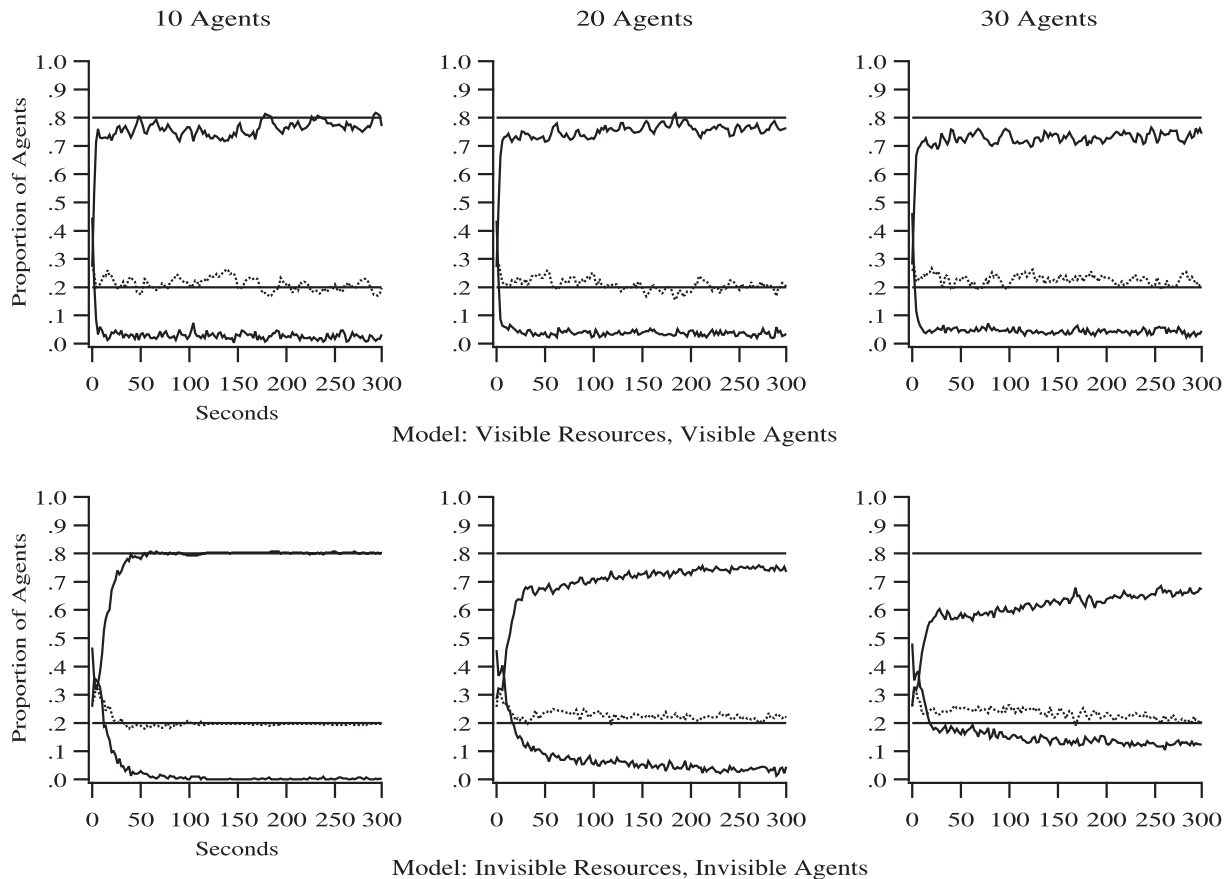


**Figure 8** EPICURE matching results for the visible (top) and invisible (bottom) 80/20 food distribution conditions with different travel distances.

tunities for the agent to change its decision and choose a pellet in the previous pool, though the goal bias tempers this change in decision. The decreased switching, in turn, promotes better matching because the new pool must appear to be consistently better in order for the agent to complete the journey. The burden of switching is higher, so agents are more likely to switch only when there is a true advantage. However, even in the visible condition, the starting location simulations showed that agents tend to correctly match the 20% pool, and undermatching seems to arise from agents leaving the 80% pool and being in neither resource pool.

### 5.3 Number of Agents

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 × 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). The constant food rate allowed us to gauge the effects of increased competition for resources caused by increasing the number of agents.



**Figure 9** EPICURE non-normalized matching results for the visible (top) and invisible (bottom) 80/20 food distribution conditions with different numbers of agents and an identical food rate. As in the previous simulations, a new piece of food is dropped every  $4/N$  seconds, but in these simulations,  $N = 20$  for all conditions.

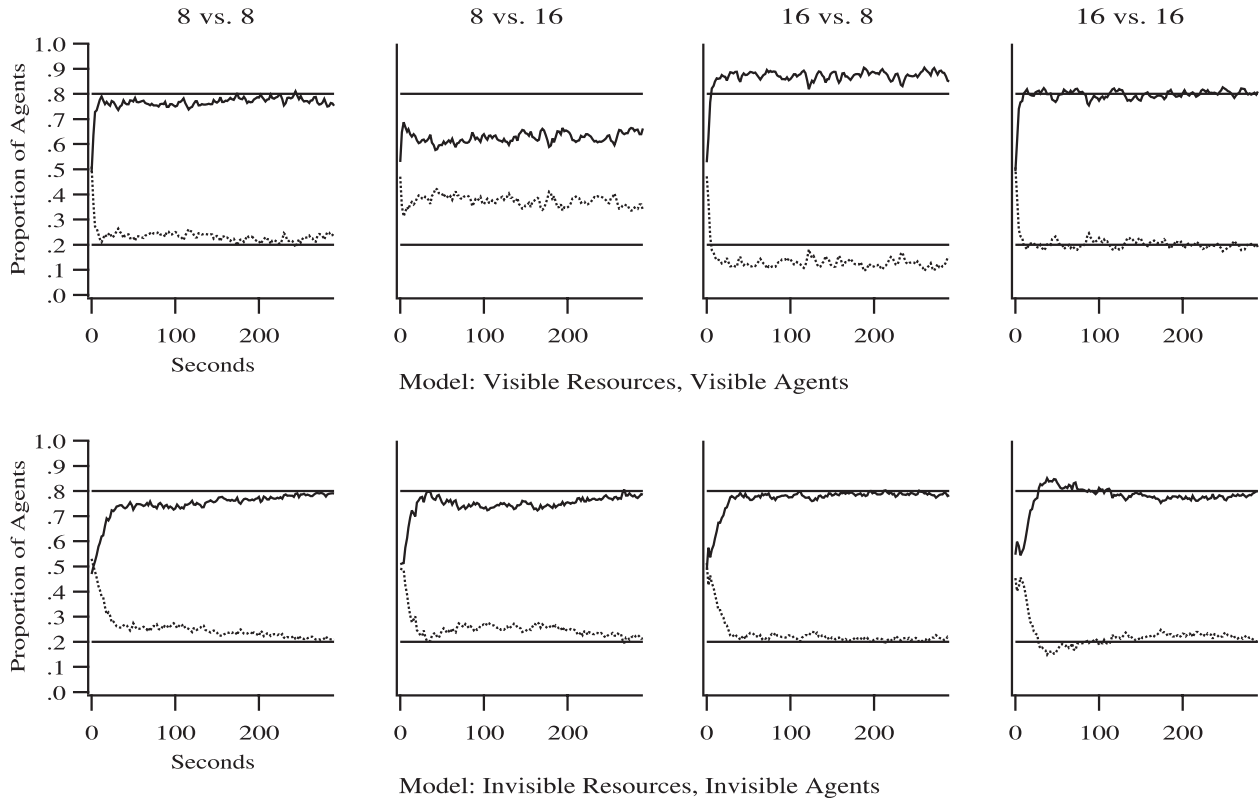
Figure 9 shows the matching results, averaged over 30 trials, for 10, 20, and 30 agents in the visible and invisible conditions. For the visible condition (in the top half of the figure), post-hoc analysis of variance (ANOVA) results indicate that 10 agents ( $M = 0.769$ ,  $SD = 0.022$ ) and 20 agents ( $M = 0.764$ ,  $SD = 0.021$ ) do not show significantly different levels of undermatching to the 80% pool, but both show significantly less undermatching than the 30 agents ( $M = 0.736$ ,  $SD = 0.028$ ) condition,  $p < 0.001$ . The differences were more extreme for the invisible condition in the bottom half of the figure, where post-hoc ANOVA results revealed a significant difference ( $p < 0.001$ ) between all three conditions [ $M = 0.808$ ,  $SD = 0.087$  (10 agents),  $M = 0.730$ ,  $SD = 0.021$  (20 agents), and  $M = 0.633$ ,  $SD = 0.013$  (30 agents)].

Thus, both the visible and invisible conditions are susceptible to greater undermatching as more agents compete for the food, but there are key differences in

the effects of the number of agents. Notably, the visible condition displays undermatching even when the food rate is effectively doubled, with 10 agents competing for the number of pellets previously given to 20 agents. This indicates that Baum and Kraft (1998) may not have increased pigeon food rates to the level at which undermatching would cease. In contrast, EPICURE shows that the invisible condition matches perfectly when 10 agents receive this double food rate, and an increase in the number of agents has greater effects on matching proportions than in the visible condition.

#### 5.4 Uniform Distributions

We also conducted simulations with uniform food distributions instead of the Gaussian food distributions used in the experiments and our previous simulations.



**Figure 10** EPICURE matching results for the visible (top) and invisible (bottom) 80/20 food distribution conditions with different uniform distribution pool sizes. In each condition, the first number indicates the radius of the 80% pool (square regions were used for simplicity), and the second number indicates the radius of the 20% pool. For example, 16 vs. 8 indicates that the 80% pool covers a total area of  $(16 \times 2) \times (16 \times 2) = 1,024$  cells while the 20% pool covers a total area of  $(8 \times 2) \times (8 \times 2) = 256$  cells.

Figure 10 shows results for both conditions, with the visible condition on top and the invisible condition at the bottom. 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 (1,024 cells compared with 256 cells), so the probabilistic food distribution is reflected by pool size.

When the pool sizes 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 may lie 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. The pools are the same size, but the 80% pool gets four pieces of food for every one piece in the 20% pool, and agents correctly distribute themselves in a four to one proportion.



The invisible condition shows a considerably different pattern. Essentially, the 8 vs. 8 and 8 vs. 16 graphs show similar degrees of undermatching, whereas the 16 vs. 8 and 16 vs. 16 graphs show nearly correct matching. This may be because many foragers in the first two cases do not receive good feedback from the environment as a few individuals can cover the 256 cells of the 80% pool relatively quickly, and although they will not do so perfectly (because the agents, like the humans, do not know the true location of each pool, and they are only sampling), they still disproportionately reduce the available information for everyone else. Meanwhile, in the latter two cases, the 80% pool is larger, so information cannot be dominated by a few individuals, and because the 20% pool receives food much less frequently, even a persistent forager in that pool does not greatly reduce the available information by sampling the area.

## 6 Discussion

EPICURE was successful in modeling the main results from the Goldstone and Ashpole (2004) and Goldstone et al. (2005) experiments, and it has given us a novel explanation of undermatching, as well as a reinterpretation of the bandwagoning results in Goldstone et al. (2005). We will discuss these two main results separately.

### 6.1 Spatial Distributions Lead to Undermatching

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 (Roberts & Goldstone, 2005). By this argument, the available resources—and hence the information available for foraging decisions—decreases 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. For example, a particular resource might be efficiently patrolled by five agents, each of whom has a “turf” of 100 cells. Additional agents tend to move out toward the less profitable periphery of a resource pool, or move to another pool.

#### 6.1.1 Agreement with Empirical Undermatching Results

In the Goldstone and Ashpole (2004) and Goldstone et al. (2005) experiments, both resource pools have equal variances, so the 20% pool occupies as much space as the 80% pool. Although more food is dropped in the 80% pool, the spatial distribution means that there does not need to be an equal increase in the number of foragers to pick up that food. The 80% pool has 4 times the productivity of the 20% pool, but they both have the same spatial extent and variance, 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, which may be due to the preponderance of models that treat foraging and probability matching as discrete choices between options (Bernstein, Kacelnik, & Krebs, 1988; Charnov, 1976; Harley, 1981; Regelman, 1984; Seth, 2002), rather than often occurring in spatially instantiated situations. Furthermore, even empirical studies overlook this interplay of food rate, number of foragers, and spatial constraints. As mentioned, Baum and Kraft (1998) obtained undermatching results even as they increased the food rate, much as in our model. However, it appears that Baum and Kraft did not use a sufficiently high feeding rate. A relatively small number of pigeons could eat the food regardless of the rate, because even at the more profitable pool, experimenters only dropped a new piece of food after the previous piece had been eaten. As a result, pigeon matching distributions did not significantly change because the rate increase did not correspondingly increase information. Another result in the Baum and Kraft study supports our spatial explanation. When the two resource pools were feeding bowls (corresponding to our 8 vs. 8 condition), the pigeons showed significantly greater undermatching than when the resource pools were larger feeding areas or elon-

gated troughs (corresponding to our 16 vs. 16 condition), which we claim provide more information to the average forager because they cannot be exploited as easily by a few foragers.

Fewer agents are needed to pick up the majority of the food in the visible than in the invisible condition. Given that agents in the latter condition must sample their environment to find the best regions, five agents cannot pick up the food very quickly, so plenty of information remains for reliable matching. As the number of agents in the invisible condition increases, it becomes likely that a few of the agents will find the pool centers and disproportionately reduce the information available to everyone else, so the agent proportions do not reflect the true resource distributions.

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. Furthermore, Gillis and Kramer (1987) found significantly greater undermatching with 240 zebrafish than with 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, but the decrease in aggression indicates that interaction history, rather than competitive ability, may have created the disparities. Note that EPICURE would predict the same results as Gillis and Kramer even if the food rate per forager stayed the same as the number of foragers increased, rather than keeping a constant rate of food as we did in our simulations of different agent populations. Ten foragers would still be able to successfully forage most of the food dropped for 30 foragers, because the spatial distribution prevents a linear information increase as more food and foragers are added.

**6.1.2 Contrasts with Other Models** The spatial constraints explanation also elucidates the conclusions drawn from Abrahams' (1986) perceptual limit model. In simulations with 2, 3, and 4 patches, Abrahams' agent populations displayed significantly more undermatching when individual agents had lower perceptual

discrimination abilities. The results arise because agents with poor perceptual discrimination must essentially choose a patch at random, which promotes uniform agent distribution. Unlike Abrahams' model, EPICURE has a spatial instantiation and shows that even if agents have perfect perceptual discrimination abilities (i.e., no perceptual limits when modeling Goldstone and Ashpole visible conditions), the foraging dynamics still create perceptual limitations via the interplay of limited space and food rate in limiting agent knowledge. Whereas Abraham claims that populations should be able to evolve better perceptual discrimination abilities to perform better, EPICURE shows that suboptimal matching can be inherent to the group dynamics.

Our spatial distribution explanation differs from Sutherland's (1983) interference model, which involves direct interactions among foragers, because we are concerned with indirect interactions in the form of resource depletion and effects on knowledge. The spatial distribution explanation also differs from the temporal variance analyses put forth as partial accounts of undermatching (Earn & Johnstone, 1997; Hakoyama, 2003). Those analyses show that properly factoring in the continuous input rate variance for the resource pools can explain some, but not all, of the undermatching in visible resource foraging experiments, but they still predict matching to the means when resources are invisible and sampling is required. Their analyses share some features of the risk-sensitivity literature (Bateson & Kacelnik, 1998), which finds that individual foragers tend to be risk averse with respect to variance in amount, but risk prone with respect to variance in time. Rita and Ranta (1998) use a renewal process model with equal competitors to demonstrate that variance in a group member's gains increases with group size, and so (assuming that foragers are risk averse with respect to variance in gains) undermatching should be expected. EPICURE demonstrates that undermatching can naturally arise from individuals' decisions. Without positing foragers' sensitivity to risk, we show that spatial constraints limit the information available for matching. Our explanation does not require variation in a forager's gains over time, and in fact, EPICURE suggests little variation over time if foragers tend to stay in the same places due to their interaction histories. However, our explanation of undermatching does rely on variation in gain among agents.

### 6.1.3 Reinterpretation of Other Empirical Results

The spatial distribution explanation offered by EPICURE and its emphasis on interaction history may also provide insights into previous foraging experiments where matching results essentially agree with the IFD. For example, Milinski (1987) conducted a series of foraging experiments in which six stickleback fish distribute themselves to two resource pools according to the IFD. In conjunction with computer modeling results that use the relative payoff sum rule from Regelman (1984), Milinski's explanation of foraging behavior relies heavily on differences in competitive abilities. When prey are conspicuous, good competitors and poor competitors use different strategies. Good competitors stay near the center of a pool, but poor competitors stay between pools waiting for prey to appear, then frequently switch between pools. Milinski notes that the IFD is nonetheless achieved because the subset of good competitors distribute themselves between pools according to the IFD, and the subset of poor competitors also distribute themselves between pools according to the IFD, but a subsequent reanalysis (Kennedy & Gray, 1993) shows that good competitors significantly overmatched to the more profitable pool ( $s = 1.23$ ) and poor competitors significantly undermatched to the more profitable pool ( $s = 0.31$ ). In any case, the competitive differences explanation is tenuous in light of Milinski's other results. He shows a strong correlation ( $r = 0.98$ ) in hunting success when the same fish are used on a second day, but he also shows that individuals essentially continue using their strategies from previous trials. For example, three frequent switchers from one trial can be combined with three frequent switchers from another trial, but none of these six individuals significantly change strategies to become more successful, low frequency switchers. Likewise, no subset of low frequency switchers becomes high frequency switchers. Thus, the high success correlation between trials may occur from repeated use of the same strategies. Similarly, pigeons have shown considerable carryover effects across trials when food is presented in predictable ratios, but little carryover when the environment is more unpredictable (Bell & Baum, 2002).

Our spatial constraints explanation provides a satisfying account of these results without resorting to competitive differences. In our account, the "good" competitors 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. Meanwhile, the "poor" competitors are those who arrive a bit later and receive less information because the early foragers exploit the pool centers. The late foragers still distribute roughly according to the IFD as they frequently switch and get prey on the periphery of each pool. The foragers' strategies thereby develop from early reward histories, but the foragers tend to use the same strategies across trials, leading to similar relative success.

Certainly competitive abilities can affect foraging success (Arak, 1983; Harper, 1982), and dominant group members are often found in the profitable center of a feeding pool (Flynn & Giraldeau, 2001). In foraging salmon, the ratio of competitive weights to resource pools has proved to fit the data much better than the IFD (Grand, 1997), and the undermatching in the abstract human foraging task with tokens has been partially explained by factoring in temporal discounting differences between participants (Critchfield & Attebery, 2003). Although Godin and Keenleyside (1984) argue that the ability to quickly assess patches may often be the competitive difference between individuals, we have shown that a sustained difference in information due to luck and early foraging history can be mistaken for a difference in abilities. One way to empirically test these explanations would be to purposefully start a subset of foragers near pool centers and subsequently compare their strategies and foraging success relative to the other foragers. It seems plausible that the two explanations will account for different phases of foraging, with competitive success initially determined by early knowledge, but differences in abilities could become the dominant factor in long foraging sessions where there is little stochastic change and everyone gradually acquires equal information.

Note that only our full model can completely account for Milinski's results with conspicuous prey. The factors from our constrained visible resources model must be combined with the memory from our constrained invisible resources model in order for some agents to find and remember the pool centers and preferentially forage there over time. Although we used the more parsimonious, constrained visible resources model to capture the data from the Goldstone and Ashpole (2004) and Goldstone et al. (2005) visible resources conditions, we agree that a more demanding foraging situation—such as a slower food rate which

requires foragers to be close to the pool in order to compete effectively—also benefits from the reinforcement history component present in the invisible model. In our constrained visible model, some foragers still become “good” competitors by virtue of being near a pool center and picking up food more quickly but, unlike the invisible condition, these foragers do not have a resulting knowledge advantage, so other foragers can see the food and compete with them in the center.

In order to propagate success across trials as found in animal experiments (Bell & Baum, 2002; Milinski, 1987; Zach & Falls, 1976), the visible condition requires a reinforcement history so the “good” competitors try to occupy the pool centers early in each trial.

## 6.2 Public and Private Information

EPICURE captured the Goldstone et al. (2005) shift in information usage in the invisible resources/visible agents condition despite maintaining a constant agent density value. When a simulation starts, the agent density factor biases agents to go to areas where other agents are foraging. Of course, only resource pools support persistent congregations, because agents must get rewards to stay in an area. Since the reward value is much larger than the agent density value, the agent’s behavior becomes primarily driven by private information once it finds a pellet. But whenever an agent is unsuccessful in finding food for a while and penalizes the local area, then the public information of agent density is again useful for exploring and finding another resource pool.

Across conditions, agent visibility shifts its role depending on the information context. It is a negative factor whenever the agent can rely on better information, such as the actual locations of visible pellets in the visible resources conditions. In these situations, the agent risks strong competition by joining the group (Sernland, Olsson, & Holmgren, 2003). When better information is not available, individuals use agent visibility as a positive factor, but only in highly uncertain circumstances where no useful private information has yet been obtained, such as the invisible resources/visible agents condition discussed above.

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. Although Valone and Giraldeau (1993)

did not find evidence that budgerigars use public information in their foraging decisions, Kendall, Coolen, and Laland (2004) found that naïve guppies conformed to prior social information, but experienced guppies made foraging decisions based on their own prior experience rather than social information. Templeton and Giraldeau (1996) have shown that starlings can observe each other’s success in order to more efficiently assess a patch. Fernandez-Juricic and Kacelnik (2004) show that starlings adjust the proportion of time they spend gazing at conspecifics based on the quality and quantity of information obtained from those conspecifics. Furthermore, individuals may use heterospecific public information as well as conspecific public information, provided that the other species share habitats and similar ecological needs (Parejo, Danchin, & Aviles, 2005). In general, a meta-analysis of social learning in animals (Laland, 2004) indicates that animals try to scrounge as an initial strategy, but they resort to social learning when scrounging is ineffective. When individuals have little information or when acquiring information is dangerous, they rely heavily on the available public information. As they develop experience and slowly accumulate private knowledge, individuals begin to eschew public information and instead act on their private information.

In fact, a recent Bayesian analysis indicates that groups should only be formed when information exchange is necessary or when there are mitigating factors such as the need for protection (Sernland et al., 2003). Otherwise, foraging alone is optimal. As group size increases, the benefit of an increasingly accurate assessment is not justified by the cost of sharing food, and the socially optimal solution is not an evolutionarily stable strategy (ESS), so solitary foragers will continue joining a group until a higher limit is reached (Clark & Mangel, 1984). Rita and Ranta (1998) use a renewal processes model to show that groups are particularly useful when the food patches are far apart or difficult to discover. In that case, the utility of social information for finding the patch outweighs the cost of sharing the resource with other group members. Accordingly, we would expect greater reliance on social information in an empirical experiment with a few large resource pools that stochastically appear and deplete in different regions of the environment, but we would expect foragers to rely on private information if those same resource pools were small and quickly depleted.

**Table 2** EPICURE predictions and empirical studies for equivalent situations.

Condition	EPICURE prediction	Empirical evidence
Visible resources, visible agents	Undermatching	Goldstone and Ashpole (2004) Kennedy and Gray (1993) Sokolowski et al. (1999)
Visible resources, invisible agents	Overmatching	Goldstone et al. (2005)
Invisible resources, visible agents	Undermatching, but find pools faster than invisible resources, invisible agents	Goldstone et al. (2005)
Invisible resources, invisible agents	Undermatching	Goldstone and Ashpole (2004)
Increased number of foragers	Increased undermatching	Gillis and Kramer (1987)
Increased distance between pools	Decreased undermatching Decreased switching	Baum and Kraft (1998) Milinski (1987)
Increased pool size or variance	Decreased undermatching	Baum and Kraft (1998)

## 7 Conclusion

We have proposed an agent-based model, EPICURE, that accurately models the group foraging results from Goldstone and Ashpole (2004) and Goldstone et al. (2005). Table 2 summarizes EPICURE's predictions and corresponding empirical evidence. After testing the model in several alternative conditions, we conclude that previous models and even empirical studies have overlooked the important interplay of spatial constraints and food rate on forager distribution. Undermatching arises because some foragers happen to sample the information first when resources are invisible, and some foragers happen to start near the pool center (essentially born with silver spoons) when resources are visible. In both cases, the early advantages actually make those foragers good long-term competitors, and their early information advantages lead to information and sampling deficiencies for the group as a whole, so undermatching arises and perpetuates. These issues become clear in the current spatially instantiated model, but they have been overlooked in previous discrete choice foraging models and even some empirical foraging studies.

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