

BRIEF REPORTS

Knowledge of resources and competitors in human foraging

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The allocation of human participants to resources was studied by observing the population dynamics of people interacting in real time within a common virtual world. Resources were distributed in two spatially separated pools with varying relative reinforcement rates (50–50, 65–35, or 80–20). We manipulated whether the participants could see each other and the distribution of the resources. When the participants could see each other but not the resources, the richer pool was underutilized. When the participants could see the resources but not each other, the richer pool was overutilized. In conjunction with prior experiments that correlated the visibility of agents and resources (Goldstone & Ashpole, 2004), these results indicate that participants' foraging decisions are influenced by both forager and resource information. The results suggest that the presence of a crowd at a resource is a deterring, rather than an attractive, factor. Both fast and slow oscillations in the harvesting rates of the pools across time were revealed by Fourier analyses. The slow waves of crowd migration were most prevalent when the resources were invisible, whereas the fast cycles were most prevalent when the resources were visible and the participants were invisible.

How do groups of people allocate themselves to resources? Do people, like many other animal species (Fretwell & Lucas, 1970), distribute themselves so as to cover resources in an approximately optimal fashion? In this work, we were particularly interested in the role of knowledge in influencing group foraging behavior. We manipulated two types of information that animals might use in determining where to allocate their foraging time. These sources of information are the distributions of resources and of other foragers.

Undermatching and Overmatching

Although the assumption of optimal foraging in groups has enjoyed some striking empirical confirmations, systematic deviations have also been reported. One common result is called *undermatching*, defined as a distribution of animals that is less extreme than the distribution of resources. When undermatching occurs, there are fewer animals at the richer patch and more animals at the leaner patch than is optimal. For example, animals may distribute themselves 75% and 25% to patches that contain

80% and 20% of the resources, respectively. Overmatching occurs if the distribution of animals is more extreme than the distribution of resources. An effective measure of matching in two-patch systems, such as those used for the present work, is the value of s in the equation

$$\log\left(\frac{F_A}{F_B}\right) = s \log\left(\frac{N_A}{N_B}\right) + b, \quad (1)$$

where the resource amounts in the patches are N_A and N_B and the numbers of foragers occupying the patches are F_A and F_B . This equation has been used for studying both individual choice (Baum, 1974) and group foraging (Kennedy & Gray, 1993) behavior. The parameter s describes the sensitivity of foragers to variations in the resource distribution, and b is a bias parameter. Optimal foraging predicts the best-fitting values of s and b to be 1 and 0, respectively. Undermatching and overmatching are obtained in Equation 1 when s is less than and greater than 1, respectively.

Undermatching is empirically found more often than overmatching. In Kennedy and Gray's (1993) meta-analysis, values of s less than 1 were found for 44 out of 52 experiments, and the mean value of s was 0.7. If we restrict our attention to the relatively few laboratory studies in which group foraging in humans has been explored, we also find consistent evidence for undermatching (Goldstone & Ashpole, 2004; Kraft & Baum, 2001; Madden, Peden, & Yamaguchi, 2002; Sokolowski, Tonneau, & Freixa i Baqué, 1999).

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Forager and Resource Information

Several empirical inquiries have explored the influence of information limits on foraging behavior. Baum and Kraft (1998) found that the presence of visual barriers that prevented pigeons from simultaneously seeing two patches had no effect on undermatching. Similarly, some studies have shown that animals make little use of other animals' foraging successes in allocating their own foraging time to patches (Valone & Giraldeau, 1993). However, other studies have shown that animals use both their personal foraging histories and vicariously obtained information from observing other foragers' successes and failures to shape their strategies and that the use of vicarious information increases with the difficulty of obtaining accurate personal information (Templeton & Giraldeau, 1996). Such vicarious information is useful in group foraging situations because one's conspecifics can act as scouts for assessing patches that one has not personally visited. Assuming that an organism uses information about the foraging success or failure of its competitors, it is clear how this information should be used. Patches where many successful foraging events have happened should be visited relatively often.

It is less clear how information regarding the sheer number of competitors should be used to guide foraging strategies. On the one hand, an animal may be attracted toward patches occupied by its conspecifics. An animal can use the prevalence of conspecifics in a patch as information that the patch is highly productive. In accord with this hypothesis, field experiments on migratory birds have shown that the presence of birds attracts other birds to the region (Pöysä, Elmgren, 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.

On the other hand, an animal may avoid sites that already have a crowd of conspecifics. Pulliam and Danielson's (1991) ideal preemptive distribution hypothesis is that the first animals to arrive in an area will take the best territory, with subsequent arrivals taking the best remaining territories. The presence of individuals at a site preempt other animals from occupying that site. Empirical evidence for this hypothesis has been obtained with aphids and plants (see Dias, 1996, for a review). One of the central questions examined in the present experiment is the following: Are people more like buzzards or aphids with respect to the influence of conspecifics on foraging strategies? Are people attracted to or repelled by crowds of other people? By using a customizable virtual world, we can dissociate the information provided by human competitors from the information provided by the resource patches. Consider the case in which the full set of foragers' locations, but not resources, is visible to each individual forager within a group. If people are attracted by crowds, there should be a tendency toward overmatching; the existence of crowds at a richer patch would lead to

even larger crowds at the patch. Alternatively, if people are repelled by crowds, undermatching is expected; the visible presence of a crowd at a rich patch would deter people from moving toward or staying in the patch.

A related question regarding population dynamics concerns periodic waves of crowding at resource patches. Goldstone and Ashpole (2004) have reported that when human foragers did not have access to the distributions of either resources or foragers, periodic population oscillations were observed. When time series reflecting the number of people in a given patch over time were submitted to a Fourier analysis, the conditions in which resources and foragers were invisible yielded pronounced population cycles of about 50 sec. One likely explanation is that an originally appealing patch would become crowded with foragers seeking to take advantage of the underused patch. This crowding would lead to relatively low payouts to the individuals making up the crowd. This, in turn, would lead to an extensive migration out of the patch, making the patch, once again, attractively underused, thereby completing one cycle of population flow. The visibility of foragers and resources was confounded in Goldstone and Ashpole's experiment, and so the present experiment also addresses the unanswered question as to whether the population cycles are due to the invisibility of foragers, resources, or both.

EXPERIMENT

We used a software system that recorded the instant-by-instant actions of individuals foraging for resources in a shared virtual environment. The participants' task was to obtain as many resource tokens as possible during an experiment. A participant obtained a token by being the first to move on top of it. The relative replenishment rates for the two pools were varied (50–50, 65–35, or 80–20). The participants either could see each other but not the entire food distribution or could see the entire food distribution but not each other.

Method

Two-hundred seventy-six undergraduate students from Indiana University served as participants in order to fulfill a course requirement. The experimental procedure largely followed that used by Goldstone and Ashpole (2004), and readers are referred there for details. The students were run on a computer in 10 groups with 32, 26, 28, 29, 27, 30, 29, 23, 21, and 31 participants. The participants were instructed to try to pick up as many "food" pieces as possible by positioning their icons on top of food locations.

The environment consisted of an 80 × 80 grid of squares. The participants controlled their positions within this world by moving up, down, left, and right, using the four arrow keys on their computer keyboards. Each participant was represented by a yellow dot. Food was gathered when a participant's position coincided with a piece of food. In the *invisible foragers, visible resources* condition, all the available food pieces were represented by green dots. When a participant picked up a piece of food, it would disappear from all the participants' screens, but the consuming participant would remain invisible. In the *visible foragers, invisible food* condition, all of the participants' locations were represented by blue dots on all the participants' screens, but food pieces were not displayed. How-

ever, if a participant picked up a food piece, the food would be displayed as a green dot on that participant's screen for 2 sec. After this time interval, the consumed food piece disappeared. Thus, the participants saw their own locations and all the other participants' locations and, occasionally, would see green dots appear when they successfully harvested pieces of food.

Every experiment was divided into six 4.5-min sessions. These six games consisted of all combinations of the two knowledge conditions and three levels of resource distribution (50/50, 65/35, and 80/20). For each of the three distribution conditions, two resource pools were constructed, with center locations at reflections and rotations of the set of coordinates {40,15} and {15, 65}. A different reflection and rotation was used for each of the six conditions, with the result that the resource centers were approximately equally likely to be in each of eight possible locations and the two centers within one session always had the same distance from one another. The order of conditions was visible food (invisible foragers) 50/50, invisible food 65/35, visible food 80/20, invisible food 80/20, invisible food 50/50, and visible food 65/35 for four of the groups and the reverse of this order for the other four groups.

The rate of food creation was based on the number of participants, with one piece of food delivered every $4/N$ seconds, where N is the number of participants. When a piece of food was delivered, it was assigned to a pool probabilistically on the basis of the distribution rate. For example, for the 80–20 condition, the food would occur in the richer pool 80% of the time and in the leaner pool 20% of the time. The location of the food within the pool followed a Gaussian distribution with a mean at the center of the pool and a standard deviation of five horizontal and vertical positions. All the food remained on the screen until it was consumed by a participant.

Results

The results indicated very modest differences between conditions as a function of their order, and so the analy-

ses were collapsed over the two orders of conditions. The distributions of participants to resources over the 4.5-min sessions are shown in Figure 1, broken down by the six conditions. This analysis includes only participants who were positioned within three standard deviations of a resource pool's center. The cutoff of three standard deviations was used as a compromise between excluding too many participants from the analysis and being too liberal in pool assignment. Using cutoffs of two, four, and five standard deviations influenced only the absolute numbers of participants consigned to pools, but not the relative percentages of participants per pool or the following Fourier analysis. For the visible and the invisible resources conditions, an average of 0.7% and 16.7% of the participants, respectively, were excluded because they were not in either resource pool. This large difference in exclusion rates was most likely due to the need for exploratory foraging in the invisible resources condition.

Horizontal lines indicate the proportions that would match the distribution of food. Figure 1 shows that the distribution of participants adjusted quickly in all conditions. For the visible resources condition, the distribution of participants overmatched the resource distribution. For the 65–35 distribution, the 65% pool attracted an average of 72.6% of the participants [$t(9) = 4.0, p < .01$]. For the 80–20 distribution, the 80% pool attracted an average of 82.4% of the participants [$t(9) = 3.1, p < .05$]. For the invisible resources (and visible agents) condition, the distribution of participants undermatched the resource distribution. For the 65–35 distribution, the 65% pool attracted an average of 61.9% of the partici-

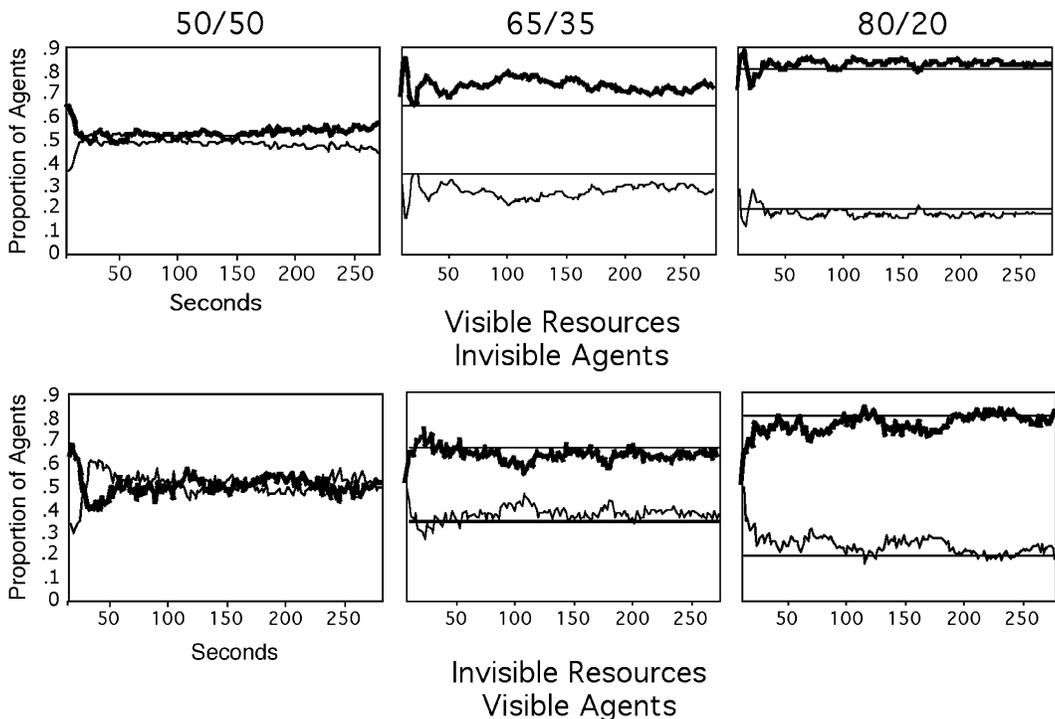


Figure 1. Changes in group sizes over the course of a session.

pants in the 50- to 270-sec interval. This value significantly deviated from 65% [$t(9) = 3.6, p < .01$]. Likewise, for the 80–20 distribution, the 80% pool attracted only 77.3% of the participants, although this value did not significantly differ from 80% [$t(9) = 2.0, p = .08$].

The overall degree of undermatching or overmatching in a condition can be measured by finding the best-fitting value of s in Equation 1 to a distribution. Figure 2 shows the relation between the logarithm of the ratio of resource distributions and the logarithm of the ratio of participant distributions. If a consistent degree of undermatching (overmatching) is found across resource distributions, a linear relation with a slope less (greater) than 1 should provide a good fit. Using a least mean square deviation method, the best-fitting values for s and b are 0.87 and 0.02, respectively, in the invisible resources condition and 1.19 and 0.10, respectively, in the visible resources condition. Both of these linear relations account for at least 95% of the variance in the participant distributions.

To explore periodic fluctuations in resource use, a Fourier transformation was applied to the time series data shown in Figure 1, broken down by individual sessions. Fourier transformations translate a time-varying signal into a set of sinusoidal components. Each sinusoidal component is characterized by a phase (where it crosses the y -intercept) and a frequency. In a frequency plot, the power at a frequency indicates the strength of a periodic response at that frequency. Figure 3 shows greater power at the relatively slow cycles around 0.02 cycles/sec for the invisible resources conditions, particularly with the 80–20 distribution. With the same 0–0.05 cycles/sec range as that used by Goldstone and Ashpole (2004), the average power for the visible and the invisible resources

conditions were 0.85 and 1.17, respectively. Treating each session's average spectral power as a single data point, the two conditions differed in their power [paired $t(9) = 3.9, p < .01$]. Low-frequency power was particularly high for the 80–20 invisible resources condition, which replicates Goldstone and Ashpole's finding of particularly elevated power for the invisible (resources and agents) 80–20 condition. For the 80–20 and 65–35 conditions, the peak power was at approximately 0.02 cycles/sec and was slightly faster for the 50–50 distribution. Pronounced power at 0.02 cycles/sec means that participants tend to create waves of relatively dense crowding at one pool that repeat about once every 50 sec.

Figure 3 also shows a second difference in the periodic cycles associated with the two visibility conditions. As compared with the invisible resources condition, the visible resources condition had higher power at relatively fast frequencies. With 0.10 cycles/sec as the boundary for high frequency, the average high-frequency power for the visible and the invisible resources conditions were 0.52 and 0.26, respectively [paired $t(9) = 4.4, p < .01$].

Discussion

The present results have implications for both the optimal distribution of people to resources and cyclic population dynamics. These implications are most clearly seen when synthesized with the results from Goldstone and Ashpole (2004). The previous study used the same experimental setup, except for testing conditions with complete visibility (both agents and resources) and invisibility. The present study completes a 2×2 factorial structure by making the visibility of resources inversely related to the visibility of agents. Table 1 presents an in-

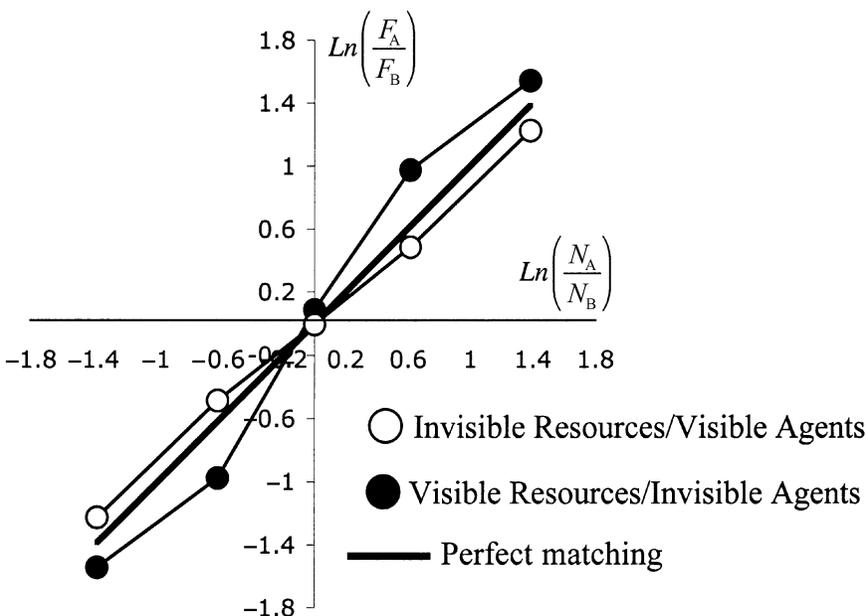


Figure 2. Comparison of resource distributions at patches A and B (N_A and N_B) with forager distributions at these patches (F_A and F_B).

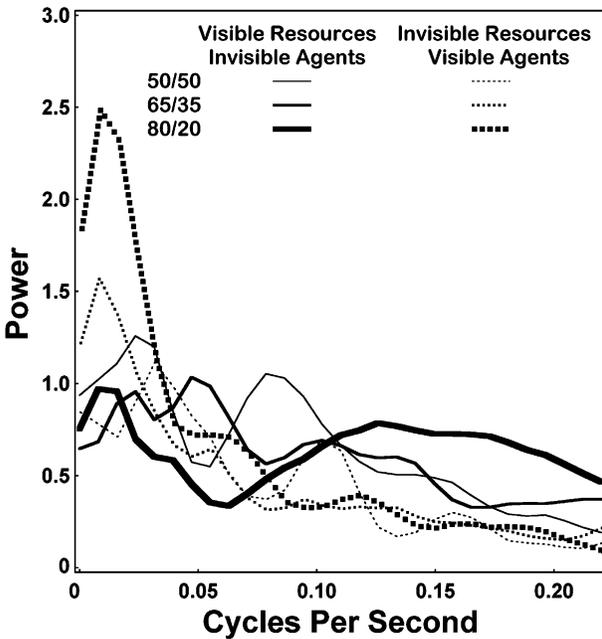


Figure 3. A Fourier analysis of group size over time.

tegrated summary of both studies. Their joint consideration allows us to isolate the effects of knowledge of agents and resources, as well as to test for interactions between these two knowledge sources.

Distribution matching. The present experiment indicates both systematic undermatching and overmatching in the distribution of human participants to resources over time. The observation of overmatching is striking because previous work on human foraging has found only undermatching (Goldstone & Ashpole, 2004; Kraft & Baum, 2001; Madden et al., 2002; Sokolowski et al., 1999). Consistent overmatching was found when resources were visible but other agents were invisible. As is shown in Table 1, undermatching was found in all other combinations of resource and agent visibility. One implication of this pattern of results is that individual

participants are sensitive to information about their competitors' locations. Table 1 reveals an interaction between resource and agent visibility, rather than just a main effect of resource visibility.

The results support the hypothesis of ideal preemptive distribution (Pulliam & Danielson, 1991), rather than conspecific attraction (Pöysä et al., 1998; Stamps, 1988). If participants had been attracted to a resource pool because of the presence of other foragers at the pool, overmatching would have been predicted with invisible resources and visible agents. That is, in a situation in which direct knowledge of resources was lacking but the popularity of a pool could be used to estimate the pool's productivity, the presence of a relatively large number of participants at the richer pool would be expected to draw still more participants to the pool. In fact, a modest level of undermatching was observed in this condition. By contrast, according to the ideal preemptive distribution hypothesis, individuals at a site preempt other individuals from occupying that site. This is consistent with the undermatching observed when agents, but not resources, are visible, and it is also consistent with the release from undermatching (i.e., overmatching) observed when resources, but not agents, are visible. By this account, overmatching is found because participants are attracted to the rich productive pools and are not dissuaded from approaching the pools by the presence of other participants (who are invisible). When both agents and resources are visible, undermatching is found. This argues for a critical role for the knowledge of agents' locations. When agents are visible at rich pools, other agents avoid the pools more than they should. Participants apparently do not adequately infer the presence of agents at rich pools when agents are invisible, or else they would avoid the rich pools, as they do when agents are visible.

The present finding of overmatching can be attributed to the specific combination of invisible agents and visible resources. Prior experiments on human foraging have involved situations in which other agents were visible (Kraft & Baum, 2001; Madden et al., 2002; Sokolowski et al., 1999). Although there has not been any precedent

Table 1
Comparison of Visibility Conditions in the Present Experiment
With Those From Goldstone and Ashpole (2004)

Agent Visibility	Resource Visibility		Characteristic
	Visible	Invisible	
Visible	Undermatching <i>s</i> = 0.78	Undermatching <i>s</i> = 0.87	Distribution
	None	≈50 sec/cycle Peak power ≈2.5	Population cycles
	Concentrated	Scattered	Population concentration
Invisible	Overmatching <i>s</i> = 1.19	Undermatching <i>s</i> = 0.68	Distribution
	≈5–10 sec/cycle Peak power ≈ 0.75	≈50 sec/cycle Peak power ≈ 6.2	Population cycles
	Concentrated	Scattered	Population concentration

for overmatching in human foraging experiments, this may be because it is atypical for resources, but not agents, to be visible. The converse condition in which agent, but not resource, information is easily available does occur frequently in nature (Stamps, 1988) and is the context for suggesting that individuals use other people as proxies for exploring strategies that they are unable to explore themselves (Boyd & Richerson, 1985). This condition is highly relevant to the question of whether people are attracted to or repelled by crowds. In contrast to situations in which conspecifics are used as vicarious sources of information of potential resources (Templeton & Giraldeau, 1996), in the present situation people are apparently repelled by crowds when resource information is not directly available. Our result is somewhat surprising given research in sociology (Chwe, 1999) and economics (Bullheimer, Dawid, & Zeller, 1998) suggesting that advantages are conferred upon individuals who “jump on the bandwagon”—who take not only their own outcomes into account when devising future strategies, but also the outcomes of their peers. In other paradigms, bandwagon and conspecific attraction effects may be obtained. Natural predictions are that crowd attraction, rather than repulsion, will be found if the time or energy required to search new areas for resources is increased or if there is decreased competition among foragers for resources within a pool.

Population cycles. There was a pronounced power peak at lower frequencies when resources were invisible and agents visible. When this result is combined with those of prior studies (see Table 1), a critical factor for low-frequency cycles is evidently the invisibility of resources. When resources are invisible, participants must rely heavily on their own harvesting rates to allocate their time to pools. One likely scenario is that random fluctuations in the forager distribution lead to a disproportionately large number of foragers in one pool. The rate of resource intake per participant then decreases due to the strong competition. Adopting a win–stay/lose–shift strategy, participants would tend to migrate out of the crowded pool because of its low utility. If this disposition to migrate affects a sizeable number of participants at roughly the same time, their departure will be roughly synchronized. The second pool will offer attractive harvesting opportunities, at least until the crowd of participants migrates to it. At some point, a crowd emerges at the second pool, leading to a disposition of several of the pools’ inhabitants to again migrate. This would lead back to the initial configuration of relatively high population density at the first pool. This entire population cycle apparently takes about 50 sec.

Goldstone and Ashpole (2004) speculated that low-frequency population cycles were caused by participants being unaware that the factors affecting their migration were indeed causing other participants to migrate. The present results provide some support for this hypothesis. When both agents and resources were invisible, the power of the low-frequency cycles was about 2.5 times greater

than it was when only resources were invisible (see Table 1). Hence, even when participants can see only each other, their inclination to depart from a crowded pool is checked, presumably because they can see that other participants have already departed from the pool. However, the still appreciable low-frequency cycles when only resources were invisible suggest that the participants were using their own reinforcement histories, rather than just the immediate information about population densities. Participants get caught up in population waves even though moving with a crowd is to their disadvantage, apparently because the same reinforcement considerations that drive their behavior also drive other participants’ behavior.

A novel result of the present experiment is the presence of high-frequency population cycles that take about 5–10 sec. These cycles are found only when resources, but not agents, are visible. In this circumstance, participants can see all food pieces as they fall, as well as the accumulated food in each pool. If one pool develops a relatively large cache of food, it is likely to be attractive to a large number of participants. However, once a crowd reaches the pool, the accumulated food will quickly be eaten, and the pool will lose its appeal because of the crowd. Apparently, the resulting migration out of the pool is again roughly synchronized. In this condition, the cycles were much faster than when resources were invisible, because the participants did not have to inductively learn about the utility of each pool but, rather, could directly observe and compare utilities. The fact that high-frequency cycles were not found when both agents and resources were visible indicates that the participants used information about each others’ locations to determine whether a resource pool was already too crowded to venture a move. Knowledge of participants can thus be used to break synchronized cycles of population change.

CONCLUSIONS

This experiment points toward both a sophisticated use of competitor and resource locations when this information is available and systematic deviations from optimal foraging. There is an imperfect match between the distributions of foragers and resources. Whether there are too many or too few foragers at a relatively rich pool depends dramatically on the knowledge available to foragers. People tend to avoid the rich pools when they can see the crowd of foragers at these pools. However, these same foragers tend to overcrowd the rich pool when only resources are visible. Perhaps most interestingly, even though people showed crowd aversion in our experiment, the Fourier time series analyses indicate that they also unwittingly traveled in crowds. Periodic population waves are significantly reduced when people have full information about the locations of other foragers. When this information is not available, the ironic consequence of people’s shared desire to avoid crowds is the emergence of migratory crowds.

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