Spatial Memory and Foraging: How Perfect Spatial Memory Improves Foraging Performance

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Abstract

Foraging is a search process common to all mobile organisms. Spatial memory can improve foraging efficiency and efficacy, and evidence indicates that many species—including humans—actively utilize spatial memory to aid in their foraging, yet most current models of foraging do not include spatial memory. In this study, a simple online foraging game was used to attempt to replicate and extend findings from a recent study (Kerster, Rhodes, & Kello, 2016) to further investigate the role of spatial memory in foraging. The game involved searching a simple 2d space by clicking the mouse to try and find as many resources as possible in 300 clicks. Spatial information was displayed that provided complete information about search history in order test how "perfect" spatial memory improves search performance. Over 1000 participants were recruited to participate in the task using Amazon's Mechanical Turk, which allowed this test to be performed across a wide parameter space of different resource distributions. Results replicated many of the findings of earlier studies, and demonstrated that spatial memory can have a dramatic effect on search performance.

Keywords: Foraging; spatial memory; Lévy walks; area restricted search; crowdsourcing

Introduction

Foraging is ubiquitous amongst living organisms, as it is a key task required for survival and procreation. Foraging is the process of searching an environment for resources, such as food or mates. While, foraging generally refers to a physical search process across a landscape, the principles involved are shared across many types of search processes, including memory search, visual search, and problem solving (Cain, Vul, Clark, & Mitroff, 2012; Rhodes, Kello, & Kerster, 2014; Rhodes & Turvey, 2007).

Some researchers have theorized that animal foraging behaviors are memory-less processes known as Lévy walks. Lévy walks are a random walk model where movement lengths are drawn from a Lévy distribution. It is unlikely that animal searches are literally random walks (Pyke, 2015), but the model captures an important aspect of foraging behavior. The distribution of path lengths, which are the lengths of straight movements made before stopping or switching directions, have been observed to follow a power law distribution. This indicates a clustered pattern of movement where a large number of smaller movements are interspersed with occasional larger movements across different scales. Lévy distributions have been observed in the foraging movements of a variety of different animals including albatrosses (Viswanathan et al., 1996), a variety of different fish species (Sims et al., 2008), and have been identified in memory search (Rhodes & Turvey, 2007) and visual search (Rhodes et al., 2014)..

Marginal value theory is an alternative approach to modeling foraging animal movements. This approach treats resources as a series of patches of varying sizes, and abstracts away the direct physical movement aspect of foraging while concentrating on optimizing the time a forager spends in a patch before moving on to another one. Marginal value theorem states that foraging can by optimized by comparing the rate of resource gain per unit time to the average rate. When the rate dips below the average, the forager should seek a new patch (Charnov, 1976).

One of the current leading models of animal foraging expands on marginal value theory by removing the spatial abstractions and implementing a model that attempts to optimize how an organism moves through the environment by relating turning rates to time since the last resource was found (Hills, 2006). Shortly after resources are found, the model turns more frequently keeping it within the resource patch. As resources become sparser, the model will turn less, propelling it on until it finds another resource and presumably another patch. This approach, known as *area-restricted search*, has recently been successful at modeling real world animal foraging data, and has been shown to generate movement patterns very similar to those generated by Lévy flight models (Hills, Kalff, & Wiener, 2013; Kareiva & Odell, 1987).

A number of studies have demonstrated that while there are some fundamental differences between animal foraging and cognitive search tasks, there are also enough similarities that findings related to foraging can be applicable to more abstract cognitive tasks. For example, Rhodes & Turvey (2007) demonstrated that times between word utterances in a category recall task follow a power law distribution as would be predicted by a Lévy walk model. Similar work has also been done from an optimal foraging perspective (Hills, Jones, & Todd, 2012). Visual search also provides a task whose constraints are similar to a foraging task, and unsurprisingly strong similarities in behavior between the tasks has been observed (Wolfe, 2013).

The successes of Lévy walks, marginal value theorem, and area-restricted search notwithstanding, spatial memory does not play a role in guiding search movements in any of these theories, i.e. there is no memory for past search locations. The exclusion of spatial memory stands in contrast with studies of animal foraging—a number of animals have been observed to utilize spatial memory for such tasks including monkeys, primates, and octopi (Garber, 1989; Mather, 1991). The lack of spatial memory in leading models of foraging helps them to be simple and tractable to analyze, but it appears that organisms with well-developed spatial memories bring those faculties to bear when engaging in a task as inherently spatial as foraging. Additionally, if spatial memory proves important to human foraging it may be informative for theories of visual search as well.

Recent work has shown evidence that humans utilize spatial memory in their search strategies. Kerster, Rhodes, & Kello (2016) demonstrated a significant effect of landmarks in a virtual foraging task. In that task, participants were presented with either a blank screen or a Hubble space image and were asked to click anywhere on the screen to search for hidden resources. Resources were non-renewing and were not correlated to the background images. Analyses of performance showed that participants were able to find significantly more resources when the Hubble images were present. The authors concluded that the images served as landmarks for searchers, aiding their spatial memory. Kerster et al. (2016) formulated a foraging model that utilizes spatial memory as one of its key features. The model produced search patterns similar to those generated by human participants, in terms of the effects of resource density and clustering on performance and search trajectories. One important difference between human participants and the model was that, even though the relative patterns of performance were similar, the model was able to find many more resources on average. The authors conjectured that this difference may be due to the model utilizing perfect spatial memory.

In the present study, we expand on Kerster et al. (2016) by testing human foraging performance under experimental conditions that mimic perfect spatial memory, akin to the foraging model that they formulated. We test whether providing a complete history of a player's past search locations and resources found will improve performance to level of the model, and how search trajectories might change with perfect spatial memory.

Methods

The experimental design used here is based on the foraging game described in Kerster et al. (2016). 1034 participants played a browser-based game written in Adobe Flash. Participants were recruited using Amazon's Mechanical Turk and were paid $0.25 for their time and participation. All data was collected during a single 24 hour period.

Participants were shown a 1280 x 1024 pixel black screen with a score counter in the top left corner which displayed the number of resources found, and a "fuel" display in the top right which displayed how many clicks they had remaining in text and with a depleting meter.

Participants were instructed to find as many resources as they could in 300 clicks, and they were able to click freely anywhere on the screen and were given visual and audio cues when they selected a location with a resource. Resources were hidden from view until found and were non-renewing. See Figure 1 for an example of what the game looks like during play.

Each participant was presented a single trial from one of 9 different resource conditions. Resources conditions were manipulated in a 3x3 design between resource density and clustering. Resource density corresponded with the total amount of resources, and was set to 100, 600, or 1100 resources. Clustering of resources was controlled using a recursive algorithm that produces power law distributions of resource clusters with varying degrees of clustering from very clustered to uniform random. The parameter controlling degree of clustering was set to three distinct levels—highly clustered (0.1), less clustered (0.3), and random i.e. not clustered (0.5).

Prior to beginning of the foraging game, each participant was presented with a short text briefing that provided instructions and framed the experiment as "space exploration." This was followed by a display showing an example distribution of resources. The example was drawn from the same condition as what they would encounter in the game, but the particular distribution shown was different than the one used during the game. Participants were also informed that, if they received a high score, they would have an opportunity to add their initials to the high score list. A high score list was used to increase participant engagement in the game. Participants then had a short practice trial (15 foraging clicks) before the game began. The whole experiment generally took less than five minutes to complete.

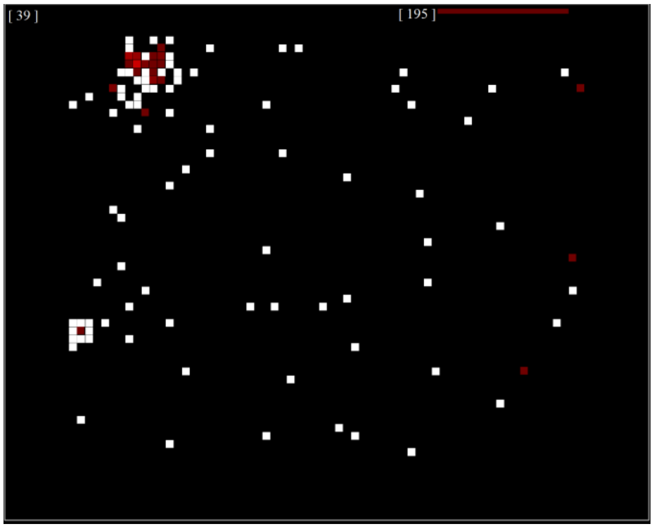
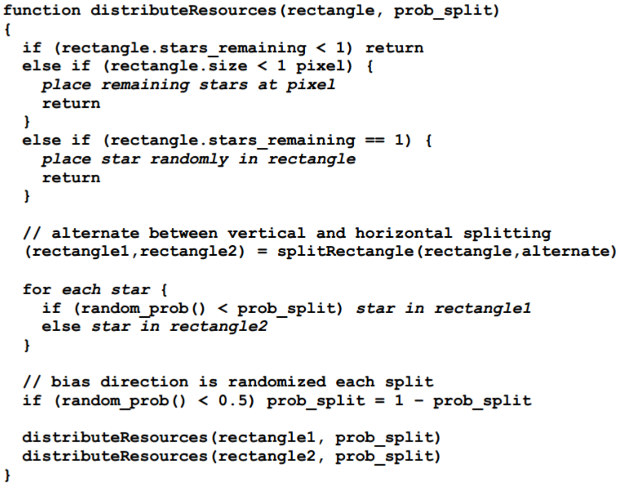


Figure 1: An example of the game's appearance during play. Squares indicate where the player has foraged thus far. White squares indicate nothing was found at that location, and red squares indicate that resources were found, with brighter shades indicating higher values. The number of resources found is shown in the upper left, and the number

of foraging clicks remaining is shown in the upper right (in numerical and bar form).

The foraging game in this experiment differed from the one used in Kerster et al. (2016) in two important ways. First, the search area was divided into an invisible grid of 15 x 15 pixel squares. Each square was searched by clicking over it, and each square could be searched only once. This restriction ensured that that there was no search area overlap among clicks, and therefore no wasted clicks searching in previously searched locations. By contrast, the game used by Kerster et al. (2016) allowed participants to click on locations that were partially or entirely searched already.



```
function distributeResources(rectangle, prob_split)
{
  if (rectangle.stars_remaining < 1) return
  else if (rectangle.size < 1 pixel) {
    place remaining stars at pixel
    return
  }
  else if (rectangle.stars_remaining == 1) {
    place star randomly in rectangle
    return
  }

  // alternate between vertical and horizontal splitting
  (rectangle1,rectangle2) = splitRectangle(rectangle,alternate)

  for each star {
    if (random_prob() < prob_split) star in rectangle1
    else star in rectangle2
  }

  // bias direction is randomized each split
  if (random_prob() < 0.5) prob_split = 1 - prob_split

  distributeResources(rectangle1, prob_split)
  distributeResources(rectangle2, prob_split)
}
```

Figure 2: Pseudocode for the recursive algorithm used to generate clustered resources. The probs_split parameter corresponds to a number between 0 and 0.5 and determines the degree of clustering, where 0 would create a single cluster, and 0.5 creates a uniform random distribution. (Kerster et al, 2016)

The other difference between Kerster et al. (2016) and the present study was the display of participant's previous searches. In the present study, a square was placed after each click on the corresponding location on the grid, and color coding was used to indicate the number of resources found, or no resources found. In particular, the range of brightness/hue levels was normalized by setting the brightest color to the maximum number of resources available in any given square, and setting white to mean that no resources were found. The restriction against overlapping clicks, plus the displayed information about previous locations foraged, effectively created a perfect external spatial memory for participants.

The game was otherwise the same as in Kerster et al. (2016), so we compare the results of the two experiments directly.

Results

Path length measures were computed using the same method described in Kerster, et al. (2016). Euclidean distances were calculated between each successive pair of clicks, and distances were summed into single path lengths for consecutive segments that had less than 10˚ of change between them. The angle threshold was used so that consecutive clicks in a relatively straight line were treated as a single path length. Each play yielded 203 path lengths on average, out of 300 clicks in total. By contrast, the average number of path lengths was 165 in Kerster et al. (2016). The increase in numbers of path lengths is likely the result of changes in foraging strategies between the two experiments (see below), as well as the transition to a fixed grid.

Path length distributions were analyzed to investigate whether they demonstrated heavy tailed properties. A number of studies have shown that the path length distributions of various foraging animals can be quantified in terms of the functional forms of their tails. Exponential, lognormal, and power law functions are commonly used, where the latter two functions feature heavier tails than exponential. Specifically, maximum likelihood methods suggested that foraging animals are sometimes best fit by power laws or truncated power laws (Humphries et al., 2010; Humphries, Weimerskirch, Queiroz, Southall, & Sims, 2012), and other times by lognormal or stretched exponential functions (Breed, Severns, & Edwards, 2015; Edwards, Freeman, Breed, & Jonsen, 2012). Additionally lognormal distributions have been fit to human foraging movements as well (Kerster, Kello, Rhodes, & Bien-Aime, 2013; Kerster et al., 2016). These heavy tailed distributions are indicative of spatial clustering in the search movements. Additionally, it has been argued that power law functions with exponents near two indicate Lévy walks, which are optimal under a certain set of assumptions (Viswanathan et al., 1999), although Lévy walks have been criticized as being overly simplified models of foraging by others (Pyke, 2015).

Aikaike's Information Criterion (Akaike, 1974) was applied to the path length distributions provided by each subject using the same methods described in Kerster et al. (2016) to determine which function best fit each distribution. Like in Kerster et al. (2016) the vast majority of distributions were best fit by the lognormal (92%). The estimated exponents also replicated, and were near the theoretically optimal exponent of 2 for Lévy walks. These findings indicate that people produced search trajectories that were inherently clustered.

Table 1: Comparison of resources found and estimated exponents across conditions between the two experiments. Standard errors are in parentheses.

This experiment replicates many of the key findings of the earlier foraging game, which then raises the question: What effect did changes in the experiment have? The model described in Kerster et al. (2016) also replicated many of these findings, but demonstrated much higher search efficiency as measured by their normalized score, i.e. proportion of available resources found. Kerster et al. proposed that the difference in score between human participants and the model was due to the model having a perfect spatial memory, and non-overlapping foraging locations. The present experiment conferred the same benefits upon human participants, so we expected a large increase in score between this experiment and Kerster et al. (2016).

	% found		Est exponent	
Density	Current Experiment	Kerster et al., 2016	Current Experiment	Kerster et al. 2016
Sparse	22.8% (0.87)	9.9% (0.81)	1.93 (0.11)	1.84 (0.16)
Medium	28.2% (0.80)	11.3% (0.90)	1.97 (0.12)	1.95 (0.19)
Dense	32.6% (0.75)	13.2% (0.88)	2.06 (0.15)	2.00 (0.16)
Clustering				
Most	55.6% (0.20)	21.7% (0.57)	1.95 (0.10)	1.97 (0.16)
Less	15.9% (0.28)	7.4% (0.23)	2.04 (0.14)	2.00 (0.17)
Random	7.0% (0.14)	5.5% (0.17)	1.98 (0.14)	1.81 (0.18)

As predicted, participants demonstrate much higher scores in the current experiment (M=16%, SD=19%) compared to the previous experiment (M=7%, SD=8%) as confirmed by a Welch's t-test (t(7142)=15.5, $p < 0.0001$). A qualitative look shows that scores in all conditions except the uniform random distribution of resources were substantially higher (see Table 1). Score is normalized by dividing the total number of resources found by the number of available resources in the condition, so that scores may be directly compared across distributions. The small difference observed for the random condition is because knowledge of prior resource locations provides no information about where to find other resources, thus spatial memory should only be useful in preventing repeated search of the same

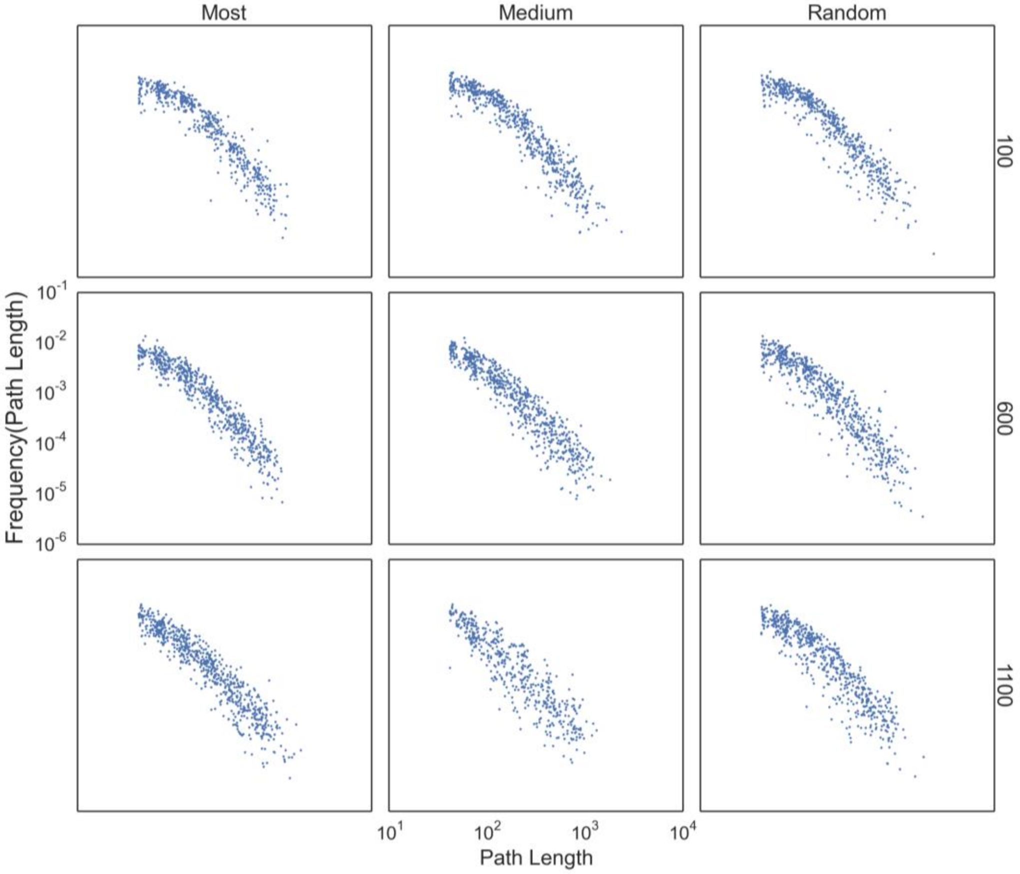


Figure 3: Path length distributions for each trial. A histogram with 10 logarithmically spaced bins was created for each trial. All trials are plotted together for each condition, separated by density and clustering. Axis labels are only displayed once, but each plot has the same axes.

location.

As mentioned earlier, two key changes were made between this experiment and the one reported in Kerster et al, 2016. Without further controls it is difficult to precisely determine how much of the increases in score were due to improvements in spatial memory, and how much were due to increased search efficiency because search locations could no longer overlap. Nevertheless, we developed a simple method to control for search efficiency by scaling normalized score by the number of unique pixels visited. This allows for the relative comparison of scores accounting for inefficiency due to repeatedly searching the same area. This analysis revealed that, for each condition except the random conditions, the majority of observed performance increases (about 70-80%) were due to improvements in spatial memory (see Table 2).

The observed increases in performance raise the question of how search trajectories changed in the present experiment due to perfect externalized spatial memory. To address this question, we used spatial Allan Factor analysis to test whether trajectories were more or less clustered in the present study compared with Kerster et al. (2016). Allan Factor analysis is designed to measure nested clustering in point processes (Allan, 1966), and was used to measure clustering in previous search tasks (Kerster et al., 2016; Rhodes, Kello, & Kerster, 2014).

Table 2: Relative increases in scores accounted for by search efficiency (lack of overlap) and perfect spatial memory

Density	**% increase due to search efficiency**	**% increase due to perfect memory**
Sparse	23.2%	76.8%
Medium	24.5%	75.5%
Dense	26.5%	73.5%
Clustering		
Most	20.3%	79.7%
Less	30.7%	69.3%
Random	77.9%	22.1%

Allan Factor analysis works by tiling the space with squares of side length L, and counting the number of points N (in this case foraged locations) within each square i. The differences between adjacent squares are averaged together, and then normalized by twice the mean.

The Allan factor statistic A(L) provides a measure of spatial variance across a number of given scales L. If foraged locations are randomly distributed then $A(L) \sim 1$ for all L. If locations are clustered across scales then $A(L) > 1$ and increases with L. If the clusters are hierarchically nested across scales then $A(L) \sim L^{\alpha}$ where $\alpha > 0$. This can be expressed as a linear relationship in log-log coordinates.

Allan Factor values A(L) were regressed across scales (L) on each distribution in log-log coordinates to produce a slope value. These values were then compared between the two experiments. Slope values are significantly higher (Welch's two-sided $T(7142)=10.7$, $p < 0.0001$), in the current experiment (M=1.12, SD=0.74) than in the distributions produced in Kerster et al. (2016) (M=0.86, SD=0.50) (see figure 4). This indicates that perfect spatial memory led to an increase in the clustering of their searches across scales.

Discussion

The current study is a direct extension of recent work using an online foraging game to explore human foraging behavior while controlling for variables that would be very difficult to control using other methods. The previous study by Kerster et al. (2016) provided evidence that spatial memory is a key feature of human foraging, and the current study confirms and extends those findings. The model used in that study uses perfect memory as a simplification as opposed to trying to implement a particular more realistic type of memory. The manner in which we give perfect to participants is also not meant to mimic any particular theory of spatial memory, but to instead explore how performance is constrained by limitations in memory. Our results demonstrated the magnitude by which foraging performance can be increased when spatial memory is improved. As long as available resources are not randomly located in the environment, search performance can be effectively doubled by providing perfect spatial memory.

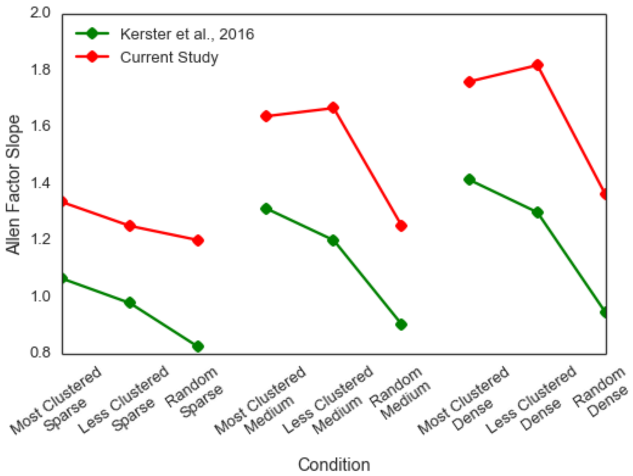


Figure 4: Comparison of Allan Factor slopes across conditions between the two experiments. Both experiments demonstrate similar patterns across condition, but the current study has higher values in all conditions, indicating more nested clustering in foraging movements.

The current study also replicated a number of important findings in the foraging literature. Notably participants generated clustered path length distributions that resemble Lévy walks. This is consistent with observations of foraging animals (Sims et al., 2008), as well as cognitive foraging tasks (Rhodes et al., 2014; Rhodes & Turvey, 2007).

In fact, Allan Factor analyses revealed that participants with perfect spatial memory showed significantly greater clustering across scales in their movements. Improved spatial memory allowed searchers to exploit information about the environment better as they uncovered it through searching. The increased clustering we observed in their movements is likely a result of improved exploitation of the clustering in the environment.

Interestingly, the increases in clustering occurred both as the resource environment became clustered, and as the density increased. The interaction effect observed here is somewhat different from that observed in Kerster, et al. (2016) and may be the result of some factors specific to the task. Further work is necessary to understand exactly how resource density, clustering, and movement constraints interact.

The simple foraging task used here is designed to have constraints in common with a variety of foraging and search tasks, and the findings presented here could be applied to many of these tasks. Some of the more interesting ramifications lie in cognitive tasks, such as visual and memory searches. Both the natural world and our memories are non-randomly distributed, which implies that knowledge of previously searched locations could be a crucial factor in efficient cognitive search.

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