INDIVIDUAL EXPLORATION AND SELECTIVE SOCIAL LEARNING: BALANCING EXPLORATION-EXPLOITATION TRADE-OFFS IN COLLECTIVE FORAGING

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Abstract

Search requires balancing exploring for more options and exploiting the ones previously found. Individuals foraging in a group face another trade-off: whether to engage in social learning to exploit the solutions found by others or to solitarily search for unexplored solutions. Social learning can decrease the costs of finding new resources, but excessive social learning can decrease the exploration for new solutions. We study how these two trade-offs interact to influence search efficiency in a model of collective foraging under conditions of varying resource abundance, resource density, and group size. We modeled individual search strategies as Lévy walks, where a power-law exponent (μ) controlled the trade-off between exploitative and explorative movements in individual search. We modulated the trade-off between individual search and social learning using a selectivity parameter that determined how agents responded to social cues in terms of distance and likely opportunity costs. Our results show that social learning is favored in rich and clustered environments, but also that the benefits of exploiting social information are maximized by engaging in high levels of individual exploration. We show that selective use of social information can modulate the disadvantages of excessive social learning, especially in larger groups and with limited individual exploration. Finally, we found that the optimal combination of individual exploration and social learning gave rise to trajectories with $\mu \approx 2$ and provide support for the general optimality such patterns in search. Our work sheds light on the interplay between individual search and social learning, and has broader implications for collective search and problem-solving.

Keywords Exploration-exploitation · Social learning · Lévy Walks · Producer-scrouter · Collective Problem-solving

1 Introduction

Foraging is essentially a problem of exploration versus exploitation. The individual forager must continually decide to either search close by and exploit known resources or head out to explore new and unknown territory. Social foragers face an additional choice once the decision to explore is made: to use social information by heading towards other foragers to scrounge their gains in knowledge or resources, or to search alone for unexplored resources. When foraging in groups, individuals must balance the explore-exploit trade-off while also deciding *how* to explore: whether by individually searching or by using information obtained by others. These trade-offs can, in turn, affect group-level dynamics that should balance the overall exploration of new resources and exploitation of the resources already found.

The use of social information and exploiting the gains of fellow foragers is a type of social learning, defined as observing and acquiring information from others. Models of collective foraging (Barnard and Sibly, 1981; Dechaume-Moncharmont et al., 2005) share much in common with more general work on social learning, which examines the trade-offs between acquiring behaviors or information by observing others versus through trial-and-error exploration (Rieucau and Giraldeau, 2011; Boyd and Richerson, 1985; Rogers, 1988; Kendal et al., 2009; Afshar and Giraldeau, 2014; Grueter and Leadbeater, 2014). Both classes of models have sought to examine the different conditions under

which social learning is more beneficial than independently searching for resources. However, the interplay between asocial search and social learning, and particularly how individual search strategies can affect the benefits of social learning, has not been addressed. Understanding the use of social information in collective search from this perspective has implications for a wide variety of systems, whether they involve humans or other animals like bees (Von Frisch, 2013), fishes (Brown et al., 2011) that use social cues to find resources in physical space or networked teams searching “problem space” for solutions to complex challenges.

In this paper, we study a spatially-explicit agent-based model of collective foraging to investigate how social foragers should balance two trade-offs, one between exploitative and explorative movements in their individual search strategy, and another between individual search and social learning. We ask how these explore/exploit trade-offs may be combined to enhance the effectiveness of social learning and group performance under different conditions like resource density and patchiness, and group size that manipulated the value and prevalence of social learning in the environment. Prior work on both classes of models has shown that social information is especially valuable when the costs of individually searching in an environment are high (Muthukrishna et al., 2016; Laland, 2004; Kendal et al., 2005), especially when resource distributions are patchy and sparse. Social learning is also beneficial when social cues are more reliable and can help to assess the quality of resources collectively, for example, in clustered or correlated resource environments (Ding et al., 2020; Clark and Mangel, 1986). However, social learning can be disadvantageous when the proportion of social learners is high and when social cues are unreliable, outdated, and bear opportunity costs (Webster and Laland, 2012). These results suggest that it is beneficial to be *selective* in when and which social information to pursue (Giraldeau et al., 2002; Laland, 2004).

Selective use of social information is necessary when too much social learning becomes detrimental. For example, finding resources after pursuing social cues may fail due to high variability in resource distributions or the strong competition present in larger groups (Smolla et al., 2015). In such cases, selective social learning can help individuals filter out costly and unreliable information (Giraldeau et al., 2002; Laland, 2004). At the group-level, excessive reliance on social learning may cause foragers to overly converge on particular locations, especially when social networks are densely connected or when there is unrestricted communication (Toyokawa et al., 2019; Bond, 2005; Barkoczi and Galesic, 2016). Selective social learning may mitigate this potential disadvantage by discouraging frequent exploitation of social information and instead allowing for individual search. Of course, the benefits of social learning also depend on the implementation of individual search behavior when social learning is not employed.

Given that individual search determines the way a group samples and explores an environment, we propose that the benefits and the optimal degree of social learning should depend not only upon the value of social information, but also on implementation of individual search strategies. For instance, explorative search behaviors can help individuals spread out and accelerate the group’s search for new resources, and lack of exploration may diminish the value of social information. We further propose that reliance on social learning can affect the trade-off between exploration and exploitation in individual search. Many theories predict that a solitary forager should balance exploration of new resources with the exploitation of the resources found to maximize their foraging returns (Krebs et al., 1978; Viswanathan et al., 1999). However, in a group, it may be beneficial for individuals to trade individual exploitation of resources for socially-guided exploitation that allows groups to aggregate and effectively search a cluster of resources. We formalize these proposals in an agent-based model to demonstrate how the explore/exploit and individual search/social learning trade-offs may interact to affect collective foraging efficiency.

2 The Model

2.1 Model Overview

We modeled the explore/exploit trade-off in individual search using a Lévy walk process. The Lévy walk is a well-studied random search model that can serve as a proxy for how individuals search or sample an environment to find resources (Viswanathan et al., 1996; Wosniack et al., 2017). At each time step, an agent takes a step in a random direction, where the size of the step is randomly drawn from a power-law distribution. The shape of the distribution and the frequency of short and long movements is determined by the parameter μ . Frequent long movements reflect an explorative search strategy, while frequent short steps reflect an exploitative strategy that focuses on searching within the neighborhood of previous locations (Billinger et al., 2014; Kauffman et al., 2000). Prior empirical and computational studies have found that $\mu \approx 2$ (Garg and Kello, 2021; Viswanathan et al., 1996; Humphries et al., 2010) can optimally balance exploration for new resources and exploitation of the resources already found in patchy environments. We tested whether the optimal value of μ changes when agents employ social learning and how different individual search strategies operationalized with different values of μ affect the benefits and optimal selectivity of social learning.

We implemented social learning as the use of cues emitted by search agents when finding resources. This form of social learning (similar to stimulus or local enhancement (Pöysä, 1992)) is widely used to increase search efficiency in various species from bees (Leadbeater and Chittka, 2007) to primates (Rapaport and Brown, 2008). In our model, social cues attracted other agents with some probability to collectively exploit the information provided by finding resources. In this way, foragers followed a *scrounger* strategy when moving toward social cues, and a *producer* strategy when searching for resources individually according to a Lévy walk process. In our model, the value of social information decreased as distance to the cue increased because resources were likely to decrease or disappear entirely in the time needed to travel the long distance. Therefore, we operationalized *selectivity* in social learning through a parameter α , which modulated the probability of scrounging as a function of distance to social cues. α also influenced the explore/exploit trade-off between individual foraging and social learning, where increased selectivity also increased the reliance on individual search. The extent of social learning was also affected by the frequency of social cues and the number of foragers pursuing them. We tested the effects of these factors on explore/exploit trade-offs by manipulating foraging group size and resource density, where larger groups with more resources produced more social cues and increased the frequency of social learning.

We measured group performance in terms of *collective foraging efficiency*, defined as the average rate of resource finding per agent and per unit distance moved. We manipulated two parameters, μ and α , that affected the explore/exploit trade-offs at the individual and social level, respectively. We also tested the advantage of selective social learning for efficient foraging (which avoids costly social cues) relative to more indiscriminate use of social learning for different conditions of μ . Finally, we tested how the degree of social learning as manipulated through these parameters affected the distribution of movement lengths and altered the original Lévy walk exponent.

Given that Lévy walks are random whereas social cues are informative, we can anticipate that responding to social cues will improve performance when resources are sufficiently clustered, but only up to a point depending on the individual search strategy and the degree of selectivity in social learning. Excessive exploitation of social cues may cause agents to overlap with each other more often and reduce exploration for new resources. This problem may be exaggerated in larger groups and avoided when the individual search is more explorative because agents are more likely to avoid overlap by “diffusing” away from each other to find unexploited resources at a faster rate. The agent-based model allowed us to examine the interplay of these factors in producing more or less efficient collective foraging behaviors.

Figure 1: Examples of the resource distributions generated by the power-law growth algorithm. The color-map indicates the density estimates (calculated using Gaussian Kernel Density Estimation) of resources present at a location. Clockwise: $N_R = 1000, \beta = 1.1$; $N_R = 1000, \beta = 2$; $N_R = 1000, \beta = 3$; $N_R = 10000, \beta = 1.1$; $N_R = 10000, \beta = 2$; $N_R = 10000, \beta = 3$.

Figure 2: **Left:** A schematic of the model. Agents (blue triangles) decide between individual exploration and using social information based on $P(s) = \exp(-\alpha d)$ to copy a resource location (green circles) found by another agent. For $\alpha > 0$, $P(s)$ will be higher for d_2 than d_1 . The level of individual exploration is dependent on μ , where $\mu \rightarrow 1.1$ results in high levels of exploration (See Supplementary Figure 1 for actual trajectories). **Right:** The effect of α and distance from another agent on the probability to use social information ($P(s)$).

2.2 Model Details

The search space was a two-dimensional $L \times L$ grid with periodic boundaries. For each simulation, the space was populated with N_R number of resources, where N_R was varied to manipulate resource density, and resources did not regenerate after consumption (i.e, destructive). We manipulated the initial spatial clustering of resources (Fig. 1) using a power-law distribution growth model. The space was initialized with 20 seed resources placed in random locations. Additional resources were placed such that the probability of a resource appearing a distance d_r from previously placed resources was given by

$$P(d) = C d_r^{-\beta} \quad (1)$$

where, $d_{min} \leq d_r \leq L$, $d_{min} = 10^{-3}$ is the minimum distance that an agent could move and $L = 1$ is the normalized size of the grid. C is a normalization constant required to keep the total probability distribution equal to unity, such that

$$C = \frac{1 - \beta}{(L)^{1-\beta} - (d_{min})^{1-\beta}} \quad (2)$$

β determined the spatial distribution of resources other than the resource seeds, such that $\beta \rightarrow 1$ resembled a uniform distribution and $\beta \rightarrow 3$ generated an environment where resources were tightly clustered. The seeds created distinct patches, and β determined the degree of clustering around those patches. The distinct patches helped generate a complex environment that was well-suited for testing collective foraging and the advantages of social learning. Each simulation was also initialized with N_A agents placed at random locations with random directional headings, where N_A was varied to manipulate group size.

On each time step, each agent consumed a resource unit if one existed within a radius, $r = d_{min}$, or in other words, if a resource was present at their current grid location. Otherwise, the agent moved in search of additional resources. The direction and distance (d) of agent movement was determined by either individual search strategy or social learning (see below). Similar to a model by Bhattacharya and Vicsek (2014, 2015), each agent was presumed to emit a signal (or cue) each time it encountered a resource within a radius of that was immediately detectable by every other agent. That is, at any given moment, agents could tell which other agents were currently on resource patches across the whole environment. An agent A_i detected the closest other agent currently on a resource, A_j . The probability of exploiting this social information and heading toward A_j was given by

$$P_S = \exp(-\alpha d_{ij}), \quad (3)$$

where d_{ij} was the distance between agents A_i and A_j , and α determined how selective an agent was in pursuing social cues in terms of distance costs and so affected how often agents pursued individual search versus social cues. $\alpha \rightarrow 0$ corresponded with minimally-selective/indiscriminate exploitation of social cues (Fig 2) where agents were

more likely to engage in social learning irrespective of distance costs. Intermediate values ($\alpha \approx 10^{-2}$) corresponded with more selective social learning, where social cue exploitation was less likely for more distant signals. And $\alpha \rightarrow 1$ corresponded with no social learning i.e., pure Lévy walks. An agent could truncate its movement before reaching its destination if it encountered a resource or another social cue. If an agent detected a social cue while already heading towards a previous one, then the agent only switched towards the new signal if the distance to the previous signal was less than that to the newly detected signal.

With the probability, $1 - P_S$, the agents followed a producer strategy and chose a target location based on their Lévy walk exponent. Individual search movements were made according to the Lévy walk model, where the heading was chosen at random and the length of movement was sampled from the following probability distribution,

$$P(d) = Cd^{-\mu} \quad (4)$$

where, $d_{min} \leq d \leq L$, $d_{min} = 10^{-3}$ is the minimum distance that an agent could move, $L = 1$ is the grid size, C is the normalization constant given by Eq. 2, and μ is the power-law exponent, $1 < \mu \leq 3$. The Lévy exponent μ modulated the search strategy as a continuum between shorter, more exploitative movements and longer, more explorative movements. Smaller values of μ correspond to longer and more frequent explorative search, whereas larger values generated shorter movements and an exploitative search strategy. The exponent $\mu = 2$ generally balances explorative and exploitative movements for maximal individual search efficiency when resources are scarce and clustered, where efficiency is the rate of finding resources per unit time or distance (Viswanathan et al., 1996). If an agent encountered resources or social cues while moving along a path given by the Lévy walk, the agent truncated its movement, and consumed the resource or followed the social cue with the probability, P_S , respectively.

Multiple agents could occupy a location simultaneously without any penalty. If multiple resources were present at a given location, agents consumed one unit of resource per time-step. If multiple agents were present at the location, they consumed the resources in the order of their arrival at the location. This feature simulated realistic conditions where pursuing distant social cues generally reduce their value. Model details are also outlined in a flowchart in the Supplementary Materials (Supplementary Fig. 2).

Each simulation ended when 30% of the resources were consumed, which ensured that the initial degree of clustering was mostly preserved throughout each simulation. Foraging efficiency η was computed as the total number of resources found divided by the average distance moved per agent. Efficiency was further normalized by dividing η by the total number of resources available (N_R) to facilitate comparisons across conditions. We varied α to take values between 0 and 1, and μ as 1.1, 2, and 3. We further simulated different conditions for resource density ($N_R = 1000, 10000$), resource distribution ($\beta = 1.1, 2, 3$), and group size ($N_A = 10, 20, 30, 40, 50$). Five hundred simulations were run for each parameter combination, and averaged results are reported. Here we report parameter values that affected explore/exploit trade-offs in individual search as well as social learning. In the supplementary materials we report results on the effects of resource environments, individual search strategies, and group sizes for groups composed of pure producers ($\alpha \rightarrow 0$) and scroungers ($\alpha \rightarrow 1$) (Supplementary Figures 8, 9).

3 Results

3.1 Social learning was more beneficial than individual Lévy walks in clustered environments

We found that when resources were clustered together (shown in lighter colors in Fig. 1), social learning ($\alpha \leq 10^{-2}$) was more beneficial than individual search driven by Lévy walks ($\alpha > 10^{-2}$, or depicted by the rightmost two points of each plot in Fig. 3). In clustered environments (in $\beta > 1.1$), the probability of finding more resources within the vicinity of a social cue was high (Fig. 1), and pursuing social cues helped agents to find resources while decreasing the costs of individual search. In contrast, individual search rather than social learning ($\alpha \geq 10^{-2}$) was beneficial in environments where resources were more dispersed across the landscape ($\beta = 1.1$) because the likelihood of encountering resources increased by random sampling and decreased after following social cues.

When resources were scarce, it was not only challenging to find resources through random individual search, but the opportunities to use social information were also far and few. We found that under these conditions, it was beneficial for agents to follow social cues irrespective of the distance costs ($\alpha \rightarrow 0$), even when resources were weakly clustered ($\beta < 3$). However, when resources were more abundant with weak clustering ($N_R = 10000$; $\beta < 3$), the benefits of minimally-selective social learning decreased compared to more selective social learning ($\alpha = 10^{-2}$). In other words, when opportunities to exploit social information were available but its value was diminished, groups benefited from trading pursuing costly social cues for more individual search.

On the other hand, groups benefited considerably from social learning when social information was more reliable in highly clustered environments with dense clusters ($N_R = 10000$; $\beta = 3$). Furthermore, it enabled a form of collective

Figure 3: Search efficiency η for $N_A = 10$ as a function of social learning parameter α , Lévy exponent μ , resource density N_R , and resource clustering β . Error bars indicate 95% confidence intervals.

Figure 4: The advantage of minimally-selective social learning ($\alpha = 10^{-5}$) relative to more selective social learning ($\alpha = 10^{-2}$) for different Lévy walks and in different resource environments. Dashed line indicates when the two levels of social learning selectivity are equivalent.

sensing where the individual agents could not only perceive resources without directly finding them, but they could also stay within the clusters to fully exploit them (Hein and McKinley, 2012). In the absence of others on a cluster, agents were more likely to exit without fully depleting the resources. Overall, these results suggest that the trade-off between individually searching the environment and socially learning about resource locations depends upon the value and prevalence of social information.

3.2 Social learning affected the optimal Lévy exponent and its benefits were maximized by explorative individual search

In our model, the agents used Lévy walks to search for resources or exploit social information by themselves. When α values were high (rightmost two points of each plot in Fig. 3), agents did not respond to social cues, and Lévy walks primarily drove individual search. Results show that Lévy walks with $\mu = 2$ were most efficient in the absence of social cues. This replicates and extends previous modeling studies showing that $\mu = 2$ implements the best trade-off for individuals between exploitative and explorative search by generating a random walk that balances long, extensive movements with small movements that resembles area-restricted search. As discussed above, when α decreased enough to drive social learning, group search efficiency for clustered resources improved substantially compared with individual Lévy walks. However, the benefits of social learning depended upon the individual search strategy, and the optimal value of the Lévy exponent shifted from $\mu = 2$.

We found that with social learning, the optimal Lévy exponent decreased and shifted to $\mu = 1.1$. In other words, it was beneficial for social learners to engage in explorative search and replace exploitative search driven by random Lévy

walks with scrounging instead, i.e. exploitative search driven by more reliable social cues. As agents responded to social information more frequently, group search became more efficient when individual search became increasingly composed of frequent exploratory, long movements with $\mu \rightarrow 1.1$. High levels of individual exploration helped groups sample the environment faster and created more opportunities for social learning. When individual exploration was lacking (for example, $\mu = 3$), social learning was not as efficient and led to only a small increase in group performance. Moreover, groups with exploitative search behavior benefited more from selective social learning relative to minimally-selective social learning (Fig.4). We explain this result in the next section.

3.3 Selective social learning was more beneficial with restricted individual exploration and abundant social information

The degree of selectivity in social learning or responsiveness to social cues in the model was controlled by α , where $\alpha \rightarrow 10^{-5}$ corresponded to a minimally-selective strategy that led the agents to follow another social signal irrespective of the costs associated with traveling long distances. A more selective strategy ($\alpha = 10^{-2}$) allowed the agents to only follow a signal if it was not very far. On the one hand, minimally-selective and frequent social learning could decrease efficiency due to long-distance movements, reducing the chances of finding resources after following a cue while increasing movement costs. On the other hand, it could also cause agents to over-exploit resource clusters by drawing too many agents while decreasing the number of agents left to explore the environment independently.

To illustrate, imagine that an agent happens upon a cluster of resources. It sends a resource signal, and another agent heads towards the cluster. They both find more resources in the cluster, and that increases the time they spend there. In turn, chances are increased of other agents responding to their signal and joining in at the cluster, and so on. This snowballing effect of agent grouping can become counterproductive if too many agents are drawn to the cluster as it is exhausted. The agents that join later at the expense of time and opportunity costs cannot find any resources left at the cluster. At the group level, the convergence of agents to a few resource clusters also impeded their ability to disperse and explore the environment for unexploited resources.

When agents' individual search strategy was closer to a Brownian walk ($\mu \approx 3$) with frequent turns and short movements, excessive use of social information led to more substantial grouping between the foragers and restricted them to small areas of the environment for longer durations (Supplementary Figure 6). Thus, a more selective social learning strategy decreased the grouping between the agents and increased group performance (Fig. 4). In contrast, when individual search strategy included fast, super-diffusive exploratory bouts ($1.1 \leq \mu \leq 2$), agents could quickly disband and disperse across the environment after depleting a resource cluster that further increased their optimality (see previous section). However, when social information was less prevalent in scarce clusters ($N_R = 1000$; $\beta = 1.1$), selective social learning was less efficient than minimally-selective social learning with high levels of exploration ($\mu = 1.1$).

We further manipulated the amount of social information available in the environment by increasing the group size of agents (N_A), where more agents increased the number of overall social cues. We found that when the number of agents or the group size increased (Fig.5, Fig.6), the benefits of minimally-selective social learning relative to selective social learning further decreased. A larger number of agents exaggerated the chances of snowballing effect that could further drive up the competition over resources, decrease the value of social cues, and reduce the individual exploration for other resources. For instance, over-exploitation of social information (from $\alpha = 10^{-5}$) in larger group sizes caused agents to aggregate together in bigger sub-groups (Supplementary Fig. 5), and for longer durations (Supplementary Fig. 6), which decreased the group-performance.

By contrast, more selective responses to social cues ($\alpha = 10^{-2}$) helped to avoid over-grouping and instead gave rise to multiple groupings around multiple clusters (see Supplementary Figures 4 (right) and 7). Multiple, simultaneous sub-grouping of agents effectively balanced collective exploration of new clusters with the exploitation of found clusters. Moreover, the advantage of selective social learning relative to minimally-selective social learning was stronger for $\mu = 3$ than $\mu = 1.1$ (Fig.6). An increase in snowballing due to larger group sizes also decreased the exploration of new resources. When agents were slow to disperse after aggregating, an increase in group size further slowed down their dispersal, and more selectivity in social learning was required to maintain exploration. This effect was further exaggerated for richer resource clusters ($N_R = 10000$).

Taken together, these results suggest that individual-level explore-exploit trade-off (given by μ) affected the optimal trade-off between individual search and social learning (given by α). If individuals had an exploitative search strategy ($\mu = 3$), it was beneficial for them to reduce exploitation of social information ($\alpha = 10^{-2}$) to maintain exploration at the group-level. Conversely, increasing exploitation of social information ($\alpha = 10^{-5}$) was beneficial for individuals that had higher explorative tendencies ($\mu = 1.1$) when social information was not abundant. However, when social cues were abundant in the environment (due to rich clusters and large groups), selective exploitation of social infor-

Figure 5: Group search efficiency η ($N_A = 50$) as a function of social learning prevalence (α) for different Lévy exponents (μ), resource density (N_R) and resource distribution (β). Error bars indicate 95% confidence intervals.

Figure 6: Effect of group size and individual search strategy on the advantage of minimally-selective social learning ($\alpha = 10^{-5}$) relative to selective social learning ($\alpha = 10^{-2}$) for $\beta = 3$. Dashed line indicates when the advantage of selective and minimally-selective social learning are equivalent.

mation was necessary to prevent groups from snowballing and effectively maintain a balance between group-level exploration and exploitation.

3.4 Combining individual exploration and social learning yielded optimal Lévy walks

Our findings that show higher efficiency at $\mu = 1.1$ compared to $\mu = 2$ pose an apparent contradiction with previous theoretical and empirical findings that have repeatedly shown the general benefits of $\mu = 2$. However, in our model, social learning modified a pure Lévy walk such that pursuit of social cues could truncate or add long movements to an individual's trajectory, and change its *observed* exponent. To test how these exponents changed with social learning and whether the observed exponents μ' resembled the theoretical optimum of $\mu = 2$, we analyzed the probability distribution of movements in the emergent trajectories under different parameters (Fig 7a (top), see Supplementary Methods for details on this analysis). We found that with an increase in social information use, exploratory walks ($\mu = 1.1$) were truncated, resulting in trajectories with μ' closer towards the theoretical optimum of 2. When resources were sparse ($N_R = 1000$), the strategies that maximized search efficiency ($\mu = 1.1$ and $\alpha < 10^{-2}$) resulted in trajectories with $\mu' \approx 1.5$ (Fig. 7a (top)). However, when exploitative area-restricted search was beneficial in dense resource clusters, the efficient trajectories were composed of shorter movements ($\mu' > 2$). This result is in line with previous findings that showed the advantages of more exploitative search in dense resource environments (Humphries et al., 2010; Kölzsch et al., 2015).

These effects were also reflected in larger group sizes (Fig. 7a (bottom)). We found that in richer resource patches ($N_R = 10000$), efficient strategy ($\mu = 1.1$ and $\alpha = 10^{-2}$) corresponded with trajectories that accommodated more

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Figure 7: **(a)** Mean estimates of observed Lévy exponents (μ') for different Lévy walks (μ), resource density (N_R) and group size (N_A) in clustered environments ($\beta = 3$). Dashed line shows the theoretical optimum of $\mu = 2$. **(b)** Correlation between search efficiency and the observed Lévy exponent for all simulations. **Top:** 10 agents. **Bottom:** 50 agents.

area-restricted/exploitative search. The formation of multiple and simultaneous groups due to a more selective social learning strategy increased the time agents had to exploit a given cluster, resulting in $\mu' > 2$. Conversely, when agents were less selective and moved longer distances only to coalesce into larger groups, a higher competition at patches decreased the time spent on exploitative/area-restricted search and decreased μ' closer to 2. Moreover, we found that when the individual search strategy was exploitative and comprised of short steps ($\mu = 3$), social learning gave rise to trajectories $\mu' \rightarrow 2$ that corresponded with high search efficiency. Pursuing social cues far away added long movements to agents' trajectories and helped them explore other areas. Taken together, these results suggest that social learning and individual exploration generated movement patterns that balanced exploration-exploitation and were close to the theoretical optimum of $\mu \approx 2$.

4 Discussion

Trade-offs between exploitation of previously found resources or solutions and exploration for new ones is fundamental to adaptive behavior in individuals and groups (Hills et al., 2015; Holland, 1992; March, 1991; Fang et al., 2010). We modeled collective foraging where agents could either learn about resources found by others and exploit them or independently search for resources by exploring and exploiting areas where resources are found. Many studies have shown that social learning can improve a group's collective capacity to find resources (Boyd et al., 2011; Kameda and Nakanishi, 2002) but when relied on excessively, it could be maladaptive in dampening exploration for new solutions. Our results show how independent exploratory search for resources and selective use of social information can enable groups to reap the benefits of social learning while minimizing its costs.

In our model, agents independently searched for resources based on their Lévy walk strategy, and they socially learned about resource locations from successful foragers under different resource environments. In line with previous studies, we found that social learning was more beneficial when resource clusters were scarce (Smolla et al., 2015; Rafacz and Templeton, 2003; Giraldeau et al., 1994; Kameda and Nakanishi, 2002; Egert-Berg et al., 2018) and difficult to find by independent/asocial search. When there was no social learning and individuals followed a pure Lévy walk, our results support previous studies (Viswanathan et al., 1996; Garg and Kello, 2021) and show that search is optimal when individuals balance the explore/exploit trade-off with the Lévy exponent of 2 ($\mu \approx 2$). When social information was available and could be effectively exploited in clustered environments ($\beta = 3$), it was optimal to replace exploitation driven by Lévy walks with exploitation driven by social cues. However, when exploration was attenuated, efficiency was increased by reducing the exploitation of social information to minimize overlap between agents.

Exploratory agents diffused quickly across the environment with minimal overlap, thereby covering territory at a faster rate. Such high diffusion rates also permitted agents to disband from others after exploiting a resource cluster and searching other parts of the environment, especially in larger groups. We found that the optimal combination between independent and random exploration, and collective and informed exploitation gave rise to trajectories with $\mu' \approx 2$. Although this result adds to vast literature on Lévy walks that show the general optimality of search patterns resembling $\mu = 2$, it also demonstrates that Lévy patterns from informed processes are more efficient than from random processes, and suggests an alternate heuristic that can be used to optimize collective search. It is possible that in natural environments and cognitive foragers, informed foraging decisions backed by memory, perception, and learning (Kerster et al., 2016; Garg and Kello, 2021) can result in similar Lévy patterns. Future models can also study informed decisions between explore/exploit and their effect on the trade-off between social and asocial learning by simulating agents with such cognitive capacities. For instance, the reliance on social cues would diminish if agents could adaptively switch between explorative and exploitative modes of searching based on prior experience, such that they engage in informed exploitative search after encountering a resource cluster and decide to explore other areas after exhausting it (Pacheco-Cobos et al., 2019; Ross et al., 2018). To shed light on more realistic aspects of social foraging, it would also be helpful to model agents that can flexibly adjust between asocial search and social learning based on the reliability and quality of social information relative to personal information integrated over prior experience (Van Bergen et al., 2004; Dall et al., 2005; Grüter et al., 2008).

The selectivity parameter in our model simulated a minimal heuristic that modulated the use of social information based on its costs, and we tested the effects of different degrees of selectivity on the benefits of social learning under varying conditions. Similar to previous studies showing the detrimental effects of social learning at the group-level when too many individuals resort to it (Barnard and Sibly, 1981; Coolen, 2002; Dumke et al., 2016), we found that excessive social learning could increase the chances of snowballing (or informational-cascades (Bikhchandani et al., 1992)), lead to large and prolonged subgroups of agents, and suppress exploration for new resources. We found that selective social learning ($\alpha \approx 10^{-2}$) “filtered” (Rendell et al., 2010) out costly and unreliable social information, and reduced overlap between agents. It also led to the formation of multiple subgroups on different resource clusters that reduced over-exploitation of resources and competition between agents, and increased the benefits of social learning. Many different mechanisms may help groups prevent over-convergence, form subgroups of optimal sizes, and increase group performance. For instance, choosing options upon which other individuals have not converged (i.e., anti-conformist social learning) (Toyokawa et al., 2019) or heterogeneity in individual strategies can prevent excessive overlap between individuals.

Theoretical and empirical studies have shown that separation and convergence between individuals can also be modulated at the individual level by adjusting local interaction rules (such as alignment with others, range of interaction or communication) depending upon the context (Hoare et al., 2004; Harpaz and Schneidman, 2020; Martínez-García et al., 2013; Beecham and Farnsworth, 1999; Warburton, 1997). Furthermore, adaptive subgrouping between individuals may also result from a “fission-fusion” social structure where groups can repeatedly disperse (i.e. fission) and re-aggregate (i.e. fusion) into subgroups and benefit from social foraging while avoiding many of the associated costs (e.g., intra-group competition) (Couzin, 2009; Grove et al., 2012b; Grove, 2012; Kummer, 2017; Garg et al., 2021). Our results predict that increased exploration after a fusion event can promote fission and increase foraging efficiency (Lardy et al., 2016). Moreover, our findings provide support to previous hypotheses about the importance of energetically-efficient exploration strategies (such as bipedalism) in promoting extensive fission-fusion and social foraging in early humans under scarce and patchy environmental conditions (Grove et al., 2012a; Isbell and Young, 1996; Kurland and Beckerman, 1985).

Although our model simulated collective foraging, its results can be generalized to shed light on the general properties of collective problem-solving. In this context, the model can be conceptualized as an interplay between individuals trying a novel solution (individual search) or emulating a successful group member (social learning) (Lazer and Friedman, 2007), in problem-spaces of varying complexity (given by the degree of resource clustering and scarcity). Under this framing, our results align with and contribute to studies on the general problem of collective search. Our results predict that higher explorative/innovative tendencies can improve a group’s problem-solving capabilities in a rugged or complex problem-space where multiple solutions need to be discovered. However, pure exploratory strategies need to be balanced with social learning in complex spaces to focus a group’s effort on the solutions already found and optimize the search (Fang et al., 2010; Miu et al., 2020; Wu et al.). By contrast, when the problem spaces are ‘simple’ (similar to $\beta = 1.1$ and $N_R = 10000$), where new solutions can be easily discovered, and multiple individuals are not needed to assess the solutions, independent exploration can be advantageous without social learning.

Our results also agree with previous studies and suggest that independent exploration can mitigate over-imitation, prevent groups from being stuck in local optima, increase informational diversity and boost group-performance (Hong and Page, 2004; Schloesser et al., 2021; Toyokawa et al., 2019). Like a densely connected group with unrestricted information-sharing, excessive levels of overall social learning in a group can decrease exploration and cause indi-

viduals to converge on sub-optimal solutions while preventing them from exploring other more profitable solutions (Giraldeau et al., 2002; List et al., 2009; Bikhchandani et al., 1992). By contrast, selective social learning mimicked partially-connected groups and helped balance global search for new solutions (or innovations) and local search near the solutions previously found. Thus, our results support previous studies on the importance of optimal connectivity and information flow in groups for problem-solving and collective behavior (Gomez and Lazer, 2019; Bernstein et al., 2018; Goldstone et al., 2013; Mason et al., 2008; Barkoczi and Galesic, 2016; Garg et al., 2021; Vining et al., 2019).

In conclusion, balancing trade-offs between exploration and exploitation of new resources or solutions is a central dilemma and shapes adaptive behavior in many biological and social systems. Our model emphasizes the interdependence between trade-offs at the levels of social learning and individual search, and shows their role in modulating the balance between overlap and diversity at the group-level. Our study has broad implications for collective behavior in distributed and social systems, general search heuristics and the effect of individual search behavior on social dynamics (Smaldino and Schank, 2012). Our model focused on group-level performance, but future studies can consider the effect of social learning on individual performances, especially if individuals differ in their propensity to explore and learn socially (Klein et al., 2017; Aplin et al., 2014; Jolles et al., 2020; Czaczkes et al., 2015). Division of labor (or task allocation) can represent another way of balancing explore/exploit trade-offs to increase group performance. Evolutionary models can test for the emergence of individual differences and task division in groups. Future models can also simulate more cognitive agents that allow for adaptive learning of social and asocial learning strategies, and shed light on the evolution of sociality, social learning, and cultural evolution.

5 Data Availability

The code to run the model is available on this Github repository - https://github.com/ketikagarg/collective_foraging. To visualize the model using Binder, follow instructions in the readme file.

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