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EVOLUTION OF EXPLORATIVE AND EXPLOITATIVE SEARCH STRATEGIES IN COLLECTIVE FORAGING

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Abstract

Keywords Lévy walks · Area-restricted search · Collective foraging · Evolutionary model · Producer-Scrounger

Evolutionary theories of foraging hypothesize that individual foraging strategies evolved to maximize search efficiency. Many studies have investigated the trade-offs between exploration and exploitation and how individual foragers manage them. However, for groups of foragers, these trade-offs can change and individual search strategies may evolve in response to their social environments. For instance, foragers may use social information to collectively find and harvest resources, which might increase competition and decrease the benefits of exploring new resources. Previous work has shown that when learning socially, it is optimal for groups to be composed of highly explorative strategies. However, individual and collective search efficiencies may not align if individual search strategies beneficial for the group are disadvantageous for the individuals. In the present study, we use an agent-based model to investigate the effect of collective foraging on the evolution of individual search strategies and how they relate to group search efficiency. We use a genetic algorithm to evolve Lévy walk exponents (μ) that govern the balance of explorative versus exploitative foraging. We show that groups can evolve with social learning whose collective performance is more optimal than without social learning. The model shows that exploiters have a selective advantage in scrounging off findings by other agents, but too many exploiters diminished group search efficiencies. We also show that social learning in large groups can increase the payoffs of exploration and lead to the selection of more exploratory groups. Finally, we show that area-restricted search can help explorers exploit found resources and lead to more efficient collective search. Our results demonstrate how exploration and exploitation must be balanced at both individual and collective levels, and how individual search strategies can evolve to the benefit of collective search efficiency.

1 Introduction

Many species, including humans, forage for resources in groups. Collective searching can decrease search costs, efficiently exploit resources, decrease variance in resource intake and enhance sensing of environmental information [Clark and Mangel, 1986, Krause et al., 2002, Berdahl et al., 2013, Harpaz and Schneidman, 2020, Roeleke et al., 2022, Aplin et al., 2014, Lihoreau et al., 2016]. It may therefore benefit individual foragers and their individual success to be part of a group [Giraldeau and Caraco, 2018, Pitcher et al., 1982]. However, this group benefit may not confer to individuals when there are discrepancies between search behavior that is adaptive for the individual versus the group [Leonard and Levin, 2022]. Foraging with a group may also affect the search strategies that are optimal for the individual. In this study, we investigate how individual search strategies evolve in the context of collective foraging, how evolved strategies impact collective search efficiency, and what factors may facilitate the evolution of efficient search strategies for individuals as well as groups.

Previous studies have shown that individual foragers must balance exploration for new resources with exploitation of known resources [Bartumeus et al., 2016, 2014, Kembro et al., 2019, Garg and Kello, 2021]. This balance may change when individuals interact and affect each other's strategies to forage as a group. For example, foragers may aggregate

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to collectively exploit a found patch of resources, but too much aggregation may prevent foragers from exploring individually to find new patches. The degree to which foragers influence each others' search strategies can depend upon how they interact, for example, through social learning.

Social learning, by which foragers can observe and acquire information about resources using social cues, can influence individual search strategies and the competition for resources. For instance, easily accessible social information and exploitation can encourage foragers to scrounge for resources. The benefits of scrounging can depend upon the properties of the physical and social environment, such as resource density and group size. Herein we will investigate how individual-level search strategies can evolve in response to constraints imposed by social learning and the foraging environment. We will also investigate the effects of evolved individual strategies on group-level search efficiency and which strategies may maximize the benefits of collective foraging.

The exploration-exploitation trade-off can shape optimal movement and search patterns in individuals [Viswanathan et al., 1996, Charnov and others, 1976]. The trade-off can be further affected by features of resources such as patch richness and travel time between patches. For instance, when patches are rich but not easy to find, exploitative search strategies that prolong a forager's time within a patch are more optimal than fast, explorative movements that cause the forager to exit a patch quickly. Conversely, if resources are not abundant, exploratory strategies that favor early departure from a poor patch can be more beneficial [Charnov and others, 1976, Krebs et al., 1978]. Therefore, it would benefit foragers to make decisions to explore or exploit based on information about the environment. Some foraging models forego the benefits of informed search in favor of cognitively simplified agents that randomly switch between exploration and exploitation [Viswanathan et al., 1996], while others base decisions to switch on information obtained while foraging [Dorfman et al., 2022, Bénichou et al., 2011, Pacheco-Cobos et al., 2019a, Hills et al., 2013, Kerster et al., 2016]. For example, area-restricted search models drive decisions to switch between exploitation and exploration based on resource encounters, which is more efficient than switching at random.

Individual foraging decisions may also be informed by the behaviors of others when foraging collectively [Strandburg-Peshkin et al., 2017, Spiegel and Crofoot, 2016, Sokolowski et al., 1997, Greene et al., 2016]. For example, if foragers can detect when and where others find resources, foragers may engage in social learning and head towards locations where others have found resources in the hopes of finding more nearby. Such social learning can decrease the need to explore resources individually and thereby reduce movement costs. However, socially-driven search strategies may also increase competition for resources and cause foragers to evolve more explorative strategies that counteract a tendency to over-aggregate and over-exploit found resource locations [Beauchamp, 2005, Gillespie and Chapman, 2001].

The effects of social learning may also interact with other search conditions such as group size and group composition to modulate the level of social information available. For example, an increase in group size can amplify social information [Detrain and Deneubourg, 2008], especially in rich environments, and accelerate the rate at which patches are depleted. Such amplifying effects of large group sizes could intensify if the foraging group is composed of slow, exploitative foragers that are likely to stay near previously found patches for longer durations [Garg et al., 2022].

Social learning may lead individuals to adopt search strategies that are not adaptive at the group level. In a previous study (Garg et al. [2022]), we showed that foraging groups could maximize their search efficiency when individual foragers independently explore the environment while selectively joining other foragers in their discoveries. However, at the individual level, such explorative strategies may not always be adaptive, especially if exploitative agents can decrease their search costs in the presence of other explorative foragers. Our conclusions in the previous paper were limited by the lack of evolutionary dynamics, as populations often fail to evolve to group-optimal equilibria due to frequency-dependent fitness effects [Rogers, 1988, Smith and Price, 1973].

In the present study, we investigated the evolution of individual search strategies along the exploration-exploitation continuum, and the effects of evolved strategies on collective efficiencies. In the previous model, all agents in a group practised the same search strategy, and we calculated which strategy maximized collective efficiency. Herein, agents could vary in their degree of exploration versus exploitation by means of a parameter μ that governed the probability of relatively short versus long movements through the resource landscape. Using an evolutionary algorithm, μ parameter values were selected on the basis of their effects on individual efficiency and in the context of different levels of social learning. Social learning was governed by a group-level parameter α that determined how likely agents were to use social information to find resources. The model does not consider the extent to which social learning (α) evolves, but rather considers the downstream evolutionary consequences of a population that relies more or less on social information. Our results show that over-reliance on social learning can promote the evolution of exploitative search strategies at the individual that are detrimental at the group level. Our results also show how informed search strategies can counteract the over-reliance on social learning by increasing the payoffs of exploratory search.

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2 Model Overview

We developed an evolutionary model of collective foraging under different conditions of resource density, group size and social learning that could constrain the evolution of individual search strategies. In the model, agents are conspecifics foraging for resources in patchy environments and their fitness is based on search efficiency. Agents can search for resources independently or they can learn about resource locations discovered by other foragers. Each simulation of the model was run until 30% of the available resources were consumed, at which point all resources were cleared and refresh, and all agents were replaced by a new generation. The new generation of agents were copied from the previous generation in proportion to the fitness of each previous agent. The new generation thereby inherited their parents' search strategies, such that the persistence of a search strategy depended on its efficiency given the search conditions.

We used the Lévy walk model ([Viswanathan et al., 1996]) to simulate a range of search strategies along the exploration-exploitation continuum. Lévy walks are governed by a power-law parameter μ that modulates the probability of relatively long versus short search movements and thereby simulates observed features of explorative and exploitative search behaviors [Mehlhorn et al., 2015]. For example, agents with $\mu \to 1$ employ a relatively large proportion of long, straight movement steps that help to cover new ground and find new patches at a faster rate compared with shorter steps that are more likely to double back on themselves. However, long steps may cause agents to exit a patch before fully exploiting its resources.

The Lévy walk model simplifies exploitative and explorative movements as different kinds of random walks. The Lévy walk model simulates the distribution of movement step sizes without the potential benefit of information that may be gained during foraging. However, foragers with memory and cognitive abilities may choose step sizes because based on information about the distribution of resources in their environments. Specifically, foragers may choose smaller movements if they have information to indicate that resources may be nearby. To test such informed search strategies, we modified the model to include area-restricted search (ARS), which is a simple heuristic that triggers slower and exploitative movements after encountering resources to search for more nearby before reverting to more wide-ranging explorative movements. ARS may increase the individual payoffs of exploratory strategies and thereby counterbalance any social learning bias towards exploitative scrounging behaviors.

3 Model Details

Similar to the model of collective foraging from Garg et al. (2022), the search space is a L x L grid with periodic boundaries. Resources in each simulation were clumped into 20 randomly-distributed patches under all conditions, and the total number of resources was varied to create either sparse or dense resource patches, $N_R = 1000$ or $N_R = 10000$ (see Supplementary Methods for more details and Fig.S7 for an example of the resource environment). Resources in the model are destructive, i.e, they are removed from the environment after being found during each simulation. We tested the model under two different number of agents, $N_A = 10$ or $N_A = 50$. Group size (N_A) varied the potential amount of social information available, and consequently the level of social interaction and competition among agents.

Each agent moves in a series of steps, where each step is defined by a heading and distance to move in a straight line. Heading and distance of each step are chosen based on either the agent's individual search strategy, or the location of a detected social cue, i.e. where another agent found one or resources on the current time step. Each agent can detect all locations where resources are found by others on each time step.

If an agent detects no social cues at the start of a given step, then pure Lévy walk agents choose a random heading and move a distance sampled from the following probability distribution,

$$P(d) = Cd^{-\mu} \tag{1}$$

where, $d_{min} \leq d \leq L$, $d_{min} = 10^{-3}$ is the minimum distance that an agent could move, L is normalized to width of the grid, and μ is the power-law exponent, $1 < \mu \leq 3$. C is a normalization constant such that

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

The Lévy exponent μ modulates the individual search strategy as a continuum between shorter, more exploitative movements and longer, more explorative movements. There were six different alleles i.e. possible values for μ: $[1.1, 1.5, 2.0, 2.5, 3.0, 3.5]$ and each agent i is characterized by one of the exponent values. $\mu \to 1.1$ represents an explorative strategy with longer steps, $\mu \to 3.5$ results in an exploitative strategy with shorter steps and frequent turns, and $\mu \approx 2$ balances the probability of long versus short steps. Later we consider ARS as an informed individual search strategy that can be added to parameterized Lévy walks.

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If an agent A_i detects a social cue at given location where another agent A_j found a resource, then the probability of A_i pursuing the social cue instead of following a Lévy walk step was equal to

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

where d_{ij} is the distance between agents A_i and A_j, and α is the social selectivity parameter that determines how selective an agent is in pursuing social information as a function of distance. If more than one social cue is detected on a given time step, the agent pursues the closest cue (with ties chosen at random). We simulated the model for three levels of social selectivity ($\alpha = 10^{-5}, 10^{-2}, 10^{0}$) that correspond with high, intermediate, and no social learning, respectively.

With high social learning, agents are more likely to pursue social cues irrespective of distance. With intermediate social learning, agents are more selective in pursuing social information and are less likely to pursue distant cues that incur greater movement costs. With no social learning, agents forage using only their individual search strategy.

Agents consume resources at locations they encounter. If multiple resources are present at a given location, agents consume one unit of resource per time step, in the order of their arrival at the location. Thus, fewer or no resources are available for agents arriving relatively late to a given resource location. An agent draws a new step and heading direction after consuming one or more resources. Agents truncate their movements towards social cues if they encounter a resource or choose to pursue a newly detected social cue. A newly detected cue is pursued only if its distance is less than that to the currently pursued cue.

Area-restricted search

As individual search strategies, pure Lévy walks are uninformed because steps are purely stochastic and unaffected by information that could be gained while foraging. We added ARS as an informed component of individual search strategies that is triggered when resources are found. Specifically, when an ARS agent moves to a location with one or more resources, it searches the vicinity before moving to its next location, where vicinity was defined as all neighboring locations within a radius of two grid cells, $r_v = 2d_{min}$. This radius is a proxy for intensive, local search upon encountering a resource that has been observed in various natural foraging conditions. ARS agents move to any and all neighboring locations where resources are found to consume them. ARS is potentially more efficient when resources are clustered and hence more likely to be near each other.

Genetic Algorithm Each simulation began with a group of agents with uniformly distributed values of μ and thus, groups represented the six alleles in equal proportions. The other three parameters (N_R, N_A, α) were held constant for each given simulation, and varied systematically across simulations. The evolutionary algorithm selects agents based on their search efficiencies η, computed as the total amount of resources consumed per total distance moved measured in grid cell lengths. Each round of selection occurs after 30% of resources are consumed, and efficiencies are normalized to assign each allele with a probability of replication proportional to efficiency.

Each new population inherits the Lévy walk exponent, μ from the selected parents. In addition, we added a mutation rate of 0.05 probability of randomizing μ to one of the six alleles for each agent on each selection round. Resources, efficiencies, and agent locations are reset after each selection round and the simulation continued anew.

Evolutionary analyses The results presented here are from 40 simulations, and each simulation was run for 3000 generations. We measured the evolved values of μ and group search efficiencies for each parameter combination and for both models (non-ARS and ARS). The results presented below show both the mean evolved μ in populations and their distribution across populations, mean search efficiencies (η), and the changes in μ and η over generations. Note that our model results in stochastic evolutionary dynamics due to variability in population sizes, resource environments, stochastic search decisions, spatial interactions, and mutations. Such stochasticity prevents the groups from evolving to fully stable equilibria [Imhof et al., 2005].

To corroborate our findings, we also performed invasion analyses with the model to test the likelihood of a strategy (μ_{mutant}) invading a population of another strategy ($\mu_{resident}$) based on their relative payoffs (see Supplementary Methods for more details). The likelihood can be shown by calculating an invasion index (i) for a given set of resident and mutant strategies,

$$i(\mu_{resident}, \mu_{mutant}) = \frac{\eta_{\mu_{mutant}}}{\overline{\eta}_{\mu_{resident}}} \tag{4}$$

If a strategy is stable, then another strategy can not outperform it and $i < 1$. If a strategy is unstable, then a mutant with a more efficient strategy can invade and $i > 1$. If two strategies μ_i and μ_j can invade each other, the groups may evolve to a stable, mixed equilibria with strategies μ_i and μ_j coexisting.

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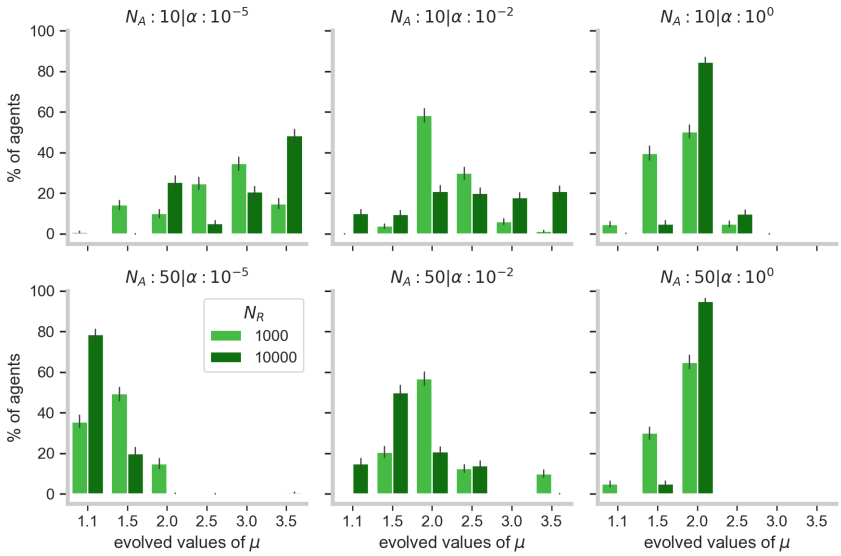
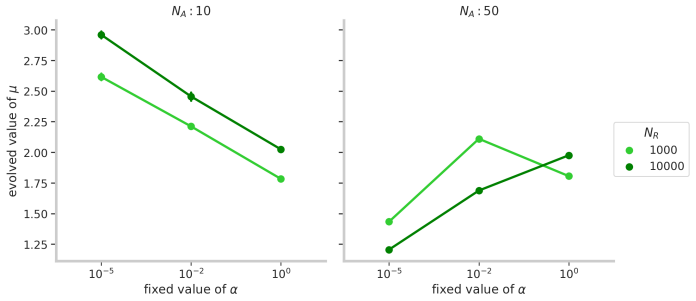
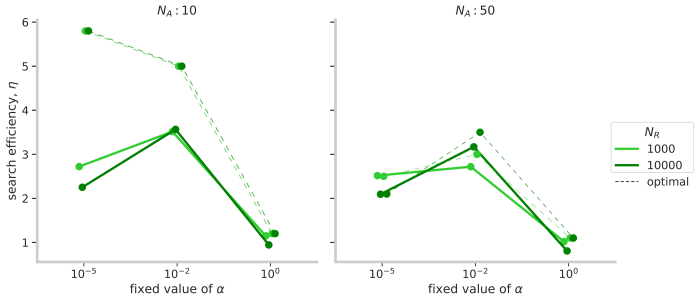


Figure 1: Distribution of the evolved values of Lévy exponents (μ) for different levels of resource density (N_R), group size (N_A) and social learning (α). α values of $10^{-5}, 10^{-2}, 10^{0}$ correspond to high, intermediate and no levels of social learning. $\mu \to 1$ corresponds to exploratory search strategy, while $\mu \to 3.5$ corresponds to exploitative search. These data represent group compositions over the last 10 generations out of a total of 3000. Error bars show 95% confidence intervals.



(a)



(b)

Figure 2: ***(a)*** Mean estimates of the evolved values of Lévy exponents (μ) for different levels of resource density (N_R), group size (N_A) and social learning (α). ***(b)*** Corresponding mean estimates of the group search efficiencies (η) of the evolved groups. Dashed lines show the maximum group efficiency value obtained in Garg et al. 2022 for given α and N_A. These values were similar for the two resource densities (N_R). The averages were taken over the last 10 generations out of a total of 3000, for every parameter combination. Error bars indicate 95% confidence intervals.

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4 Results

4.1 Reliance on social learning leads to less efficient mixed groups of explorers and exploiters.

Previous studies have shown that with little or no social learning (i.e, solitary foraging), individual search strategies that balance explorative and exploitative movements with the Lévy exponent, $\mu \approx 2$ are optimal for individual and group-level search efficiencies [Viswanathan et al., 2008, Garg et al., 2022, Bartumeus et al., 2016]. We similarly found that without social information, the genetic algorithm increased search efficiency by selecting individual search strategies with $\mu \approx 2$ (Figs. 1, (right column) and 4 (top-left) and Fig. 8(right)). However, when foraging steps were guided by social cues as well as individual search strategies, mean group efficiency fluctuated and decreased over generations instead (Fig. 8(left)).

In the presence of social information and high levels of overall social learning, our previous model [Garg et al., 2022] showed that explorative individual search strategies can maximize group-level search efficiencies. The model also showed that exploratory search can increase the rate at which resources are discovered while decreasing excessive aggregation at patches. However, here we found that the genetic algorithm was unable to select the optimal individual strategy when agents could use information ($\alpha < 10^0$) from their group members. Instead, the algorithm selected μ distributions that fluctuated between explorative and exploitative strategies over generations, with an exploitative bias (see Fig.1 (top-left)).

The fluctuation in distributions of individual search strategies with social learning can be explained by a cyclical evolutionary dynamic. Beyond some proportion of explorative strategies, exploitative strategies become advantageous because they can scrounge off the explorers. But as exploitative strategies are increasingly selected, the proportion of explorative strategies drops and they become over-exploited. Exploitative search becomes less efficient and the advantage swings back to explorative strategies, and so on. This cyclical dynamic is similar to negative frequency-dependent selection that can lead to a mixed evolutionary stable strategy between explorers and exploiters–exploiters are more efficient when their frequency is low in the population and as a result neither explorers or exploiters can completely invade a population. We can also see this pattern in the invasion analyses (Fig. S10 (top-row)) where exploitative mutants could invade explorative populations, but exploitative populations could in turn be invaded by explorers with $\mu = 1.5$.

The changes in the group composition due to frequency-dependent selection also affected the group-level search efficiency. Higher proportions of exploitative search corresponded with lower efficiencies. For example, in Figs. 3a and 4 (top row), the mean μ of the group (shown in blue) decreased and increased periodically, and the decreases in μ coincided with elevated search efficiencies (shown in green). As explained above, an increase in explorers made the group and exploiters more efficient searchers. Exploiters could then replace explorative agents, but at the expense of mean efficiencies. This effect caused dips in mean efficiency to coincide with increases in mean values of μ. As a result of high levels exploitation, evolved groups were substantially less efficient than the optimal search efficiencies predicted in Garg et al. 2022 (shown with dashed lines in Fig.2b).

We also found that the degree of exploration and exploitation can depend on resource density. When resource patches were richer ($N_R = 10,000$), the value of discovering new resources diminished relative to greater exploitation of rich patches. As a result, the overall values of μ were higher in richer patches than in scarcer patches (Fig. 2a), and groups frequently evolved to be composed of highly exploitative agents ($\mu \geq 3$) (Fig. 1). This effect further diminished group-level search efficiencies due to lower rates of resource discoveries and restricted group-level exploration (Fig. 2b). In addition to the social selectivity parameter and resource density, group size can also affect the level of social learning as discussed next.

4.2 Excessive social learning in large groups increased the advantages of explorative strategies and maintained optimal levels of group-level search efficiencies.

Larger group sizes may increase the availability of social information and thereby increase social learning and the level of competition faced by agents. We found that in large groups ($N_A = 50$), explorative search strategies were more likely to be selected than exploitative ones (Fig. 2a (right), Fig. 1 (bottom panel)). The presence of more agents in a group led to more persistent social cues and caused the group to excessively aggregate to the point of compromising search efficiency. As a result, patches depleted more quickly and competition between agents increased. Under such conditions, explorative strategies ($\mu \to 1$) had higher payoffs than exploitative strategies. Longer movements with less turns not only increased the rate of discovery of new patches but also helped agents exit patches before others could join. On one hand, in larger groups, the higher frequency of explorative agents increased the rate of resource discovery leading to even higher payoffs. On the other hand, exploitative agents who arrive later to a patch find resources are

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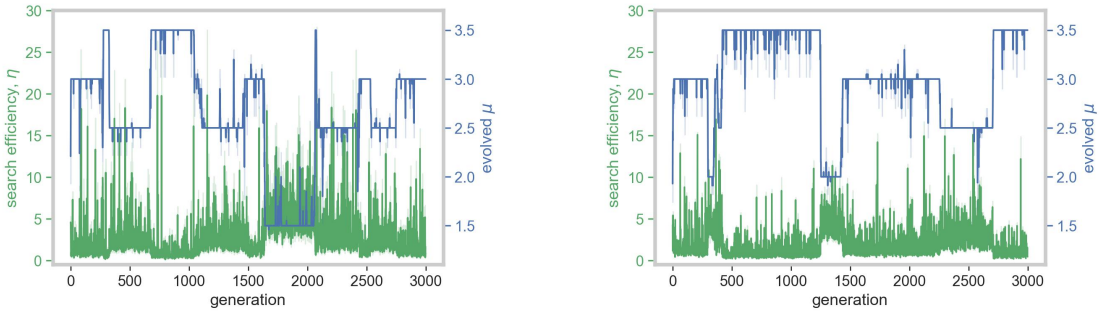

(a) $N_R = 1000$ (b) $N_R = 10000$

Figure 3: Example of an evolutionary trajectory of the mean value of a group's μ (in blue) and η (in green) over 3000 generations for a single simulation of a group of size 10 with $\alpha = 10^{-5}$. The shaded regions indicate 68% confidence intervals of the mean estimates.

already exploited and are thus less efficient. As a result, explorative strategies ($\mu \approx 1.1$) were less likely to be invaded by exploitative strategies under high levels of social learning ($\mu \geq 2.5$) (Figs. 1, S11).

At the group level, higher proportions of explorers corresponded with near-optimal search efficiencies (Fig. 2b (right)) as derived from the previously published model. The advantage of highly explorative strategies further increased in richer patches ($N_R = 10,000$), contrary to the effect for small groups (see previous section). In large groups, richer patches initiated a 'snowballing' phenomenon where social information was over-amplified due to agents spending longer times in patches. As a result, groups evolved to be even more explorative (Fig. 1) in richer patches. However, snowballing was less likely to occur with selective use of social information ($\alpha = 10^{-2}$). When social cues were pursued selectively, aggregation and subsequent competition at patches decreased and shifted mean μ values to be more exploitative (Fig. 2a (right)). In other words, when few agents could join at a resource patch and social interaction was low, either due to small groups or intermediate social selectivity, exploitative search strategies increased search efficiency by prolonging time spent in patches.

Taken together, our results so far show that social learning can negatively affect the evolution of explorative and exploitative strategies by reducing the frequencies of explorative agents and thereby diminishing search efficiency. While explorative tendencies were determined by resource density, social learning and group size, invasion analyses showed that search strategies with $\mu \approx 2$ are least likely to be invaded by other strategies, on average and across all conditions (see Fig.S12). These results hold when modeling individual search strategies as parameterized Lévy walks, but as they are random and uninformed, one might expect different results when individual search strategies can adapt to found resources. Next, we add ARS as a component of individual search that exploits found resources and may therefore alter the selection and evolutionary dynamics of individual search strategies.

4.3 Area-restricted search promotes the selection of explorative search strategies that are more optimal with social learning.

In the results discussed thus far, Lévy walks with explorative μ exponents were not competitive with social scrounging because they were unable to exploit found resources. ARS should enable explorative foragers to individually exploit found resources by engaging in local search when resources are found. The addition of an area-restricted search component to the model could change the optimal search efficiencies both at the individual and the group level. To test this hypothesis, we added ARS to the model in Garg et al. 2022. With pure Lévy walks and no social learning, $\mu = 2$ was optimal search behavior because search movements are a mix between long, explorative steps and short, exploitative ones. But with ARS, explorative agents can adaptively switch to exploitative steps after encountering resources and may not need short steps otherwise. Indeed, with ARS added, $\mu = 1.1$ resulted in randomly oriented explorative movements mixed with informed exploitative bouts and optimal search efficiencies (Fig. S13). The mix also increased search efficiencies (Fig. S13) for all values of μ and α when compared to pure Lévy walks, and selective social learning was more beneficial with ARS than without it.

In the evolutionary model, we found that ARS led the genetic algorithm to select more explorative search strategies that adaptively engaged in local search when resources were found. As a result, it was less effective for exploitative agents to scrounge from their explorative counterparts and mean μ values decreased below 2 (Fig. 5a) with fewer exploiters selected (Fig. 6). In addition, fluctuations in μ were smaller with ARS than without it (Fig. 4 (bottom row)). Due to higher proportions of explorative agents, the evolved groups maximized their search efficiencies (Fig. 5b) close to

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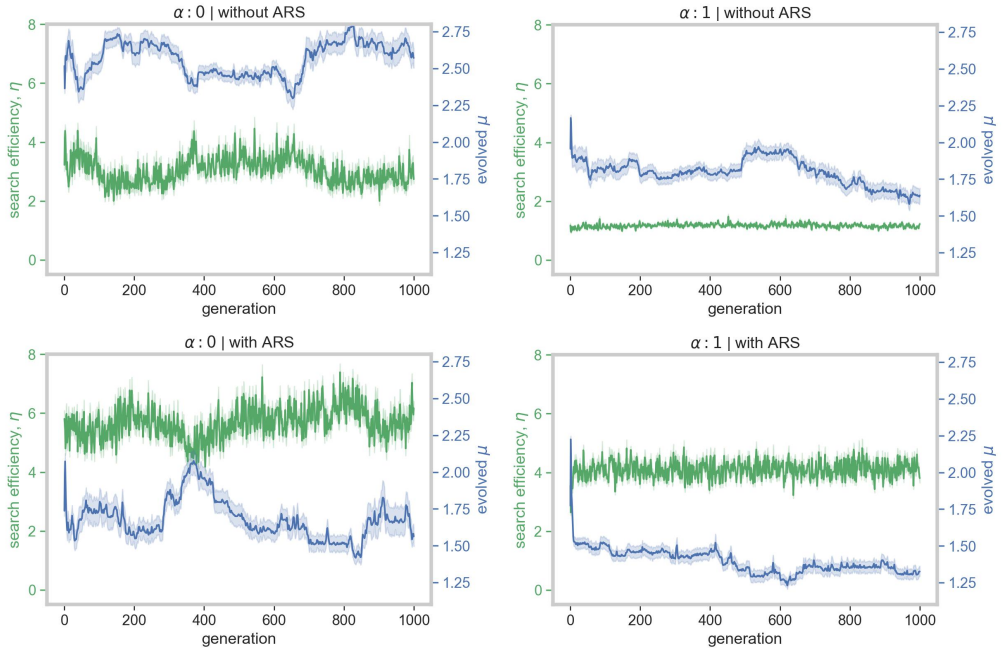
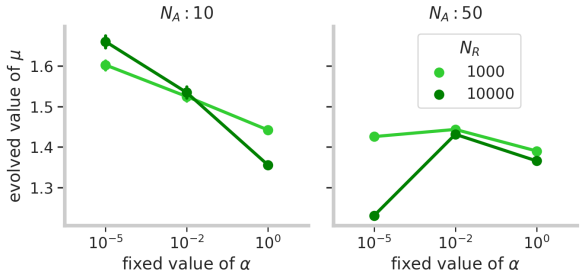
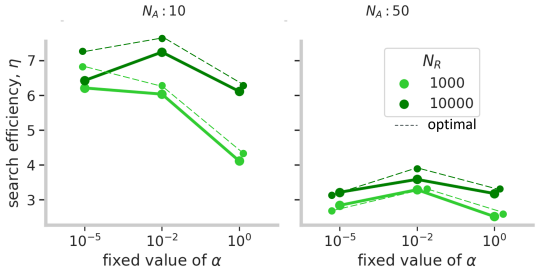


Figure 4: Time-average of trends over all simulations in efficiency, η and Lévy exponent, μ over 1000 generations for groups of size, 10 and $N_R = 1000$. We calculated moving average of window size of 20 generations to show clearer trends. The shaded regions indicate 95% confidence intervals of the mean estimates.



(a)



(b)

Figure 5: ***(a)*** Mean estimates of the evolved values of Lévy exponents (μ) from the area-restricted search (ARS) model for different levels of resource density (N_R), group size (N_A) and social learning (α). ***(b)*** Corresponding mean estimates of the group search efficiencies (η) of the evolved groups. The averages were taken over the last 10 generations out of a total of 3000, for every parameter combination. Error bars indicate 95% confidence intervals.

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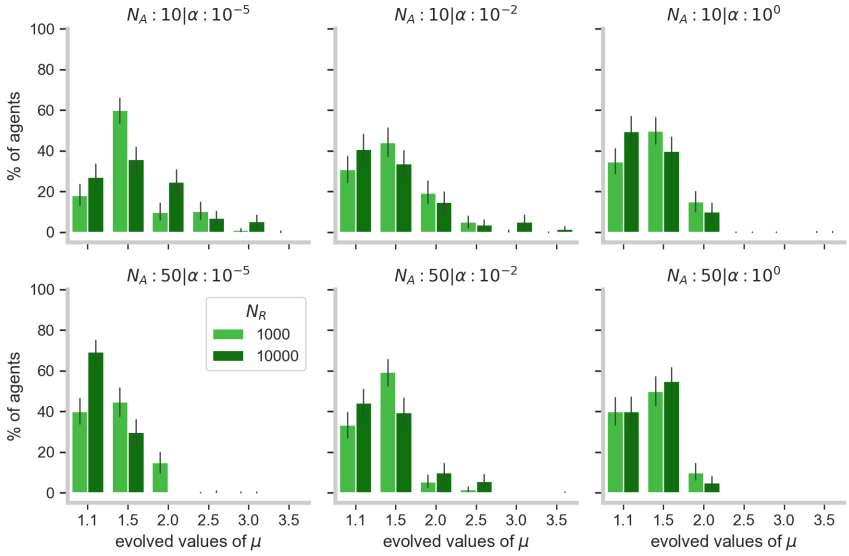

Figure 6: Distribution of the evolved values of Lévy exponents (μ) for different levels of resource density (N_R), group size (N_A) and social learning (α). These data represent group compositions over the last 20 generations out of a total of 3000. α values of $10^{-5}, 10^{-2}, 10^{0}$ correspond to high, intermediate and no levels of social learning. $\mu \to 1$ corresponds to exploratory search strategy, while $\mu \to 3.5$ corresponds to exploitative search. The error bars indicate 95% confidence intervals.

the theoretical optimum (shown in dashed lines in Fig. 5b) as estimated from the model reported by Garg et al. 2022. Moreover, unlike the non-ARS condition where social-learning led to a decrease in search efficiency over generations (Fig. 8), foragers using ARS became more efficient (Fig. 9).

Similar to the non-ARS condition, the level of exploration practised by groups decreased with the use of social information. But as social learning became excessive, for example in large groups, groups became highly explorative. This effect was strongest with dense patches, where the average μ was even lower with no social learning ($\alpha = 0$). When resource patches were plentiful and they could be effective exploited with ARS, it was beneficial for large numbers of agents to spread out and decrease competition [Di Bitetti and Janson, 2001]. Finally, due to the higher proportion of explorers in evolved groups, mean group-level search efficiencies (Fig. 5b) were close to the theoretical optimum (shown in dashed lines).

ARS with $\mu \to 1$ can resemble non-ARS Lévy search with $\mu \approx 2$. The difference between the two lies in whether information about the environment drives the decision to switch between exploring and exploiting or whether the switch occurs randomly. Results from invasion analyses (Fig. 12) show that, on an average and across conditions, Lévy walks with $\mu \approx 2$ were least likely to be invaded by exploiters or explorers. Taken together, our results indicate that search strategies that balance exploration and exploitation, whether by informed or random decisions, can be evolutionary stable with social learning.

5 Discussion

Optimal search and foraging models have mostly focused on solitary foraging, where a forager has to balance explorative and exploitative modes of search to discover and harvest resources [Viswanathan et al., 1996, Bartumeus et al., 2016, Charnov and others, 1976]. Our model shows that the evolution of individual search strategies, in terms of exploration and exploitation, can depend upon social interactions among foragers in groups. The model also shows how strategies selected for foraging efficiency at the individual level may not always be beneficial for collective foraging. Instead, individual-level selection can lead to discrepancies between individual and collective search goals Leonard and Levin [2022] by favoring less-efficient exploitative strategies. We found that informed Lévy-like patterns such as those generated by ARS can restore and stabilize the balance between exploration and exploitation at both individual and group levels. Such a balance can improve both individual and collective search efficiencies, and result in the evolution of more optimal search groups.

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Previous models have shown that Lévy-like search strategies can be optimal for individual foragers, especially when information about the environment is lacking [Bartumeus et al., 2014, Viswanathan et al., 1996, Garg and Kello, 2021]. We found that pure Lévy strategies do not lead to efficient search for groups of foragers in which information about found resource locations is shared between foragers. Instead, the presence of social learning requires a concomitant increase in the role of cognitive processing in individual search strategies to maintain and enhance search efficiency. Our results add to previous studies showing how the addition of simple heuristics to random-walk models can greatly increase search efficiencies when compared to purely random search models [Hills et al., 2013, **?**]. Results also suggest that minimizing the role of cognitive processing will tend to underestimate the extent to which non-local search is explorative. Indeed, random search models might be especially insufficient to capture real-world behavior under conditions of threat and competition. Under such conditions that pose significant opportunity costs, foragers face additional pressures to search efficiently and they can not afford to search randomly [Mobbs et al., 2018].

Evidence for simple heuristics like ARS has been found in humans and other animals [Pacheco-Cobos et al., 2019b, Wiesner et al., 2012, Dorfman et al., 2022]. Our results suggest that ARS may confer an evolutionary advantage to social foragers by increasing their share of resources. Furthermore, ARS patterns (i.e., short, exploitative bouts alternating with longer excursions) can closely resemble Lévy patterns of $\mu \approx 2$ and be more efficient than a pure Lévy process where the switch between exploration and exploitation is random. Thus, our work adds another ultimate explanation to the persistence of Levy-like patterns across species and conditions [de Jager et al., 2011]. Given that our results show that on an average, $\mu \approx 2$ is the strategy that is least likely to be invaded across all conditions (Fig.S12), our results support the hypothesis that intrinsic Lévy processes [Kölzsch et al., 2015, Sims et al., 2019] can be bet-hedging strategies to stabilize equilibria in groups [Campeau et al., 2022].

In our previous paper [Garg et al., 2022], we showed that collective search can be efficient if individual foragers are highly explorative and quickly find new resources, while being selective in their social learning to exploit and collectively exploit clusters of resources found. Herein we showed social learning requires foragers be more intelligently exploitative to protect their efforts from scrounging. Other studies on social foraging have shown that foragers may use certain strategies to increase their finder's share [Di Bitetti and Janson, 2001, Vickery et al., 1991]. For instance, capuchin monkeys maintain large distances between each other while searching for food, in order to harvest a sufficient amount of food share before others join in. Likewise, in our model, exploratory foragers with ARS were better at finding resources and maintaining distances between each other. Different social systems may employ other mechanisms to protect from scrounging and more generally promote exploration, such as social prestige or synchronized food-sharing in hunter-gatherers [Winterhalder, 1996]. Multi-level selection, where foragers compete with each other but also face group-level pressures to cooperate, can also give rise to competitive groups that maintain a high proportion of explorers for higher efficiencies.

Our results show that the level of social learning practised by the group can also determine the search strategies of individuals. Excessive social learning increased the proportion of explorers within a group, resulting in theoretically optimum groups. For example in large groups, where social cues were over-amplified, exploitative strategies had low payoffs. The late-arriving exploiters were not able to find many resources left in a patch and thus, were selected against the fast moving explorers who could quickly exit a patch before facing diminishing returns. Similar to our model's predictions, studies of bees have shown that the level of exploration practised by the bees increases with group size, due to competition for limited resources [Grüter and Hayes, 2022]. However, our model assumes that the tendency or ability to make foraging decisions on the basis of social information is independent of the individual search strategy. It is possible that these search features maybe correlated [Kurvers et al., 2010], in which case, groups would benefit from a mix of asocial explorers that find resource patches and social exploiters who harvest a found patch. The movement or space-use patterns can also affect how foragers acquire information (e.g., due to speed-accuracy trade-offs) [Spiegel and Crofoot, 2016] or how well they can communicate with each other [Roeleke et al., 2022]. Further investigations can modify the model's assumptions to test these effects of exploratory strategies on group-level efficiencies and general adaptability.

Individuals in many animal groups can consistently differ from each other in their search strategies, especially in terms of explorative behavior [Reader, 2015, Mehlhorn et al., 2015], that in turn can affect group-level behaviors related to foraging such as cohesiveness, flocking, risk-taking[Aplin et al., 2014, Ioannou and Dall, 2016, Ward et al., 2004, Dyer et al., 2009, Burns and Dyer, 2008]. Our work adds to this discussion and shows instead how the differences between individuals in their exploratory tendencies may be affected by physical and social environment features. We show that the differences in the movement speed and patch discovery can lead to dynamics similar to the classic producer-scrounger models [Barnard and Sibly, 1981, Caraco and Giraldea, 1991]. Our results support previous empirical work that have shown exploratory and exploitative foraging behavior to be density-dependent [Sokolowski et al., 1997, Greene et al., 2016]. Our model also suggests that these differences may not always be adaptive, and a high proportion of exploiters can decrease the mean fitness of a population. Although a mix of explorers and exploiters in a group was not theoretically optimum in our model, that may not always be the case in the natural world. In some

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socially foraging species, where individual fitness is tightly linked with that of the group, exploratory scouts do not optimize their finder's share and instead abandon food sources after discovering and recruiting other workers [Grueter and Leadbeater, 2014, Liang et al., 2012]. In many natural conditions, explorative strategies may have additional risks (such as predation, high search costs or reduced attention to social cues) that could decrease efficiencies in groups composed solely of explorers. For instance, in a variable environment, if the most rewarding option is associated with high risk, then explorers that continue searching for better options would be selected against [Arbilly et al., 2011]. Furthermore, maintaining a mix of diverse search strategies may be especially helpful in variable and uncertain resource environments [Dingemanse et al., 2004].

Studies on optimal search strategies have largely focused on the individual-level and how physical environment can shape the strategies. The present work shows that the studies on optimal search strategies need to account for the social environment, as well. We show that an individual's search behavior is constrained by both the physical and social environment, and can, in turn, shape the group and its capabilities. Our model also highlights how the differences between random and informed search strategies can lead to important consequences on both individual- and collective-level search efficiencies, especially under competitive foraging. Future models on social foraging should account for the role social information plays in shaping individual preferences and search behavior, and how social learning is affected by independent search behavior. In this paper, we used the explorative-exploitative movements to highlight these trade-offs but social foraging models can easily extended to other aspects of search behavior such as optimal departure time, optimal travel time that are formulated within the Marginal Value Theorem framework [Davis et al., 2022]. For instance, decisions to explore or exploit can be driven by the perceived value of resource patches that can be modeled to take into account the costs and benefits of both the physical and social context [Silston et al., 2021].

The implications of our results are not limited to foraging for resources, but extend to collective problem-solving and action, where independent searchers use social information to find solutions to a problem. Studies on collective problem-solving and search can benefit from investigating how individual search behavior within a group might be influenced by the strategies adopted by others. For instance, if some group members are risk-prone and explorative, then others might prefer searching less-riskier solutions, minimize their search costs, and prefer to improve upon solutions found by others. Or being a part of a group may dilute risk and embolden group members to explore for novel and risky solutions to a problem [Camisón-Zornoza et al., 2004]. There may be additional incentives for exploration for novel solutions or ideas, for example, patents, social prestige, and other rewards associated with innovations [Giraldeau et al., 2017]. Our results also suggest that studies on collective behavior should consider the discrepancies between individual and collective goals, costs and benefits [Leonard and Levin, 2022]. Further, investigating how social learning and communication evolve in tandem with individual search strategies under different contexts can shed light on general aspects of collective behavior and sociality.

6 Author Contributions

K.G, C.T.K. and P.E.S contributed to the conception and design of the model, wrote and edited the paper; K.G. coded and analyzed the model.

7 Data Availability

Code is available on this Github repository - `https://github.com/ketikagarg/collective_foraging`.

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8 Supplementary Methods

8.1 Resource Environment Generation

We generated resource environments (Fig.S7) 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

$$P(d) = C{d_r}^{-\beta} \tag{5}$$

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

$$C = \frac{1-\beta}{(L)^{1-\beta} - (d_{min})^{1-\beta}} \tag{6}$$

β determines the spatial distribution of resources other than the resource seeds, such that $\beta \to 1$ resembled a uniform distribution and $\beta \to 3$ generated an environment where resources were tightly clustered. In this paper, we set $\beta = 3$ to generate distinct resource patches.

8.2 Evolutionary Invasion Analysis

We systematically tested whether a population of composed of agents with a given μ can be invaded by a mutant agent with another value of μ. To perform invasion analysis, we simulated homogeneous populations of a $\mu_{resident}$ ranging between 1 and 3.5, and for each of the resident populations, we added a mutant with another value of μ_{mutant} between 1 and 3.5. Each of these populations was run for only one generation (i.e., they did not evolve), and we tested the

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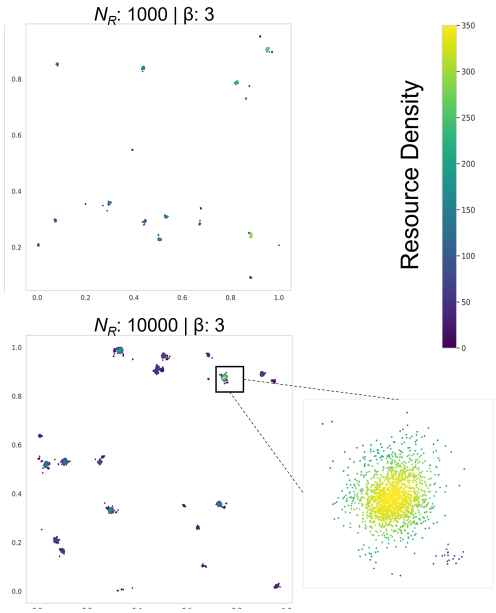

Fig.S7: Examples of the resource distributions generated by the power-law growth algorithm with $\beta = 3$. The color-map indicates the density estimates (calculated using Gaussian Kernel Density Estimation) of resources present at a location.

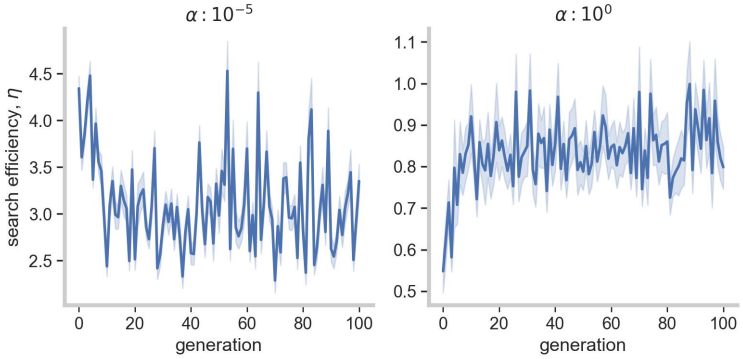

Fig.S8: Average trends in collective search efficiency over initial generations, for the non-ARS condition, group size of 10 and resource density of 10,000. The figure shows that in the absence of social learning ($\alpha = 10^0$), search efficiency of the group increases, but with social learning ($\alpha = 10^{-5}$), search efficiency decreases. Note the different y-axes limits for the two panels.

likelihood of a given μ_{mutant} invading $\mu_{resident}$ by calculating an invasion index, i, for a pair of two different values of μ where:

$$i(\mu_{resident}, \mu_{mutant}) = \frac{\eta_{\mu_{mutant}}}{\overline{\eta}_{\mu_{resident}}} \tag{7}$$

9 Supplementary Figures

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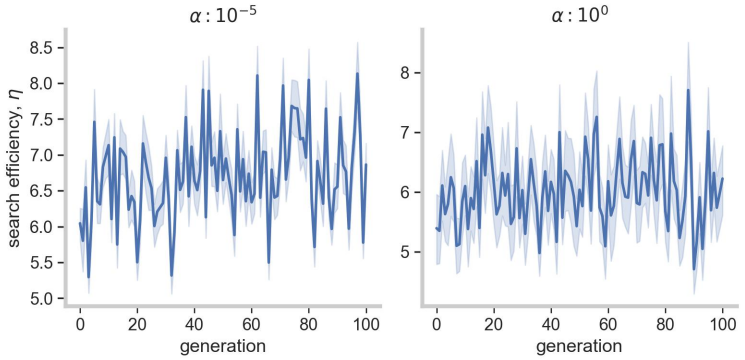

Fig.S9: Average trends in collective search efficiency over initial generations, for the ARS condition, group size of 10 and resource density of 10,000. The figure shows that with and without social learning, search efficiency of the group increases over time. However, with social learning ($\alpha = 10^{-5}$), the increase is more substantial than without ($\alpha = 10^{0}$). Note the different y-axes limits for the two panels.

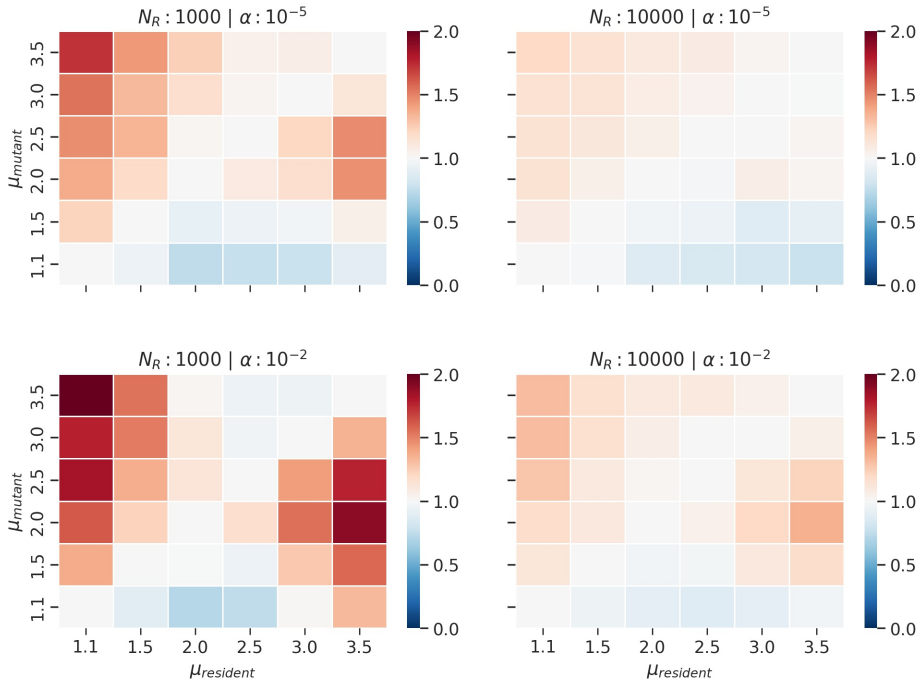

Fig.S10: Mean estimates of invasion index for groups of size 10, different levels of resource density (N_R) and social learning (α) over 500 simulations. Index values greater than 1 imply that the mutant μ will be over to invade the resident μ.

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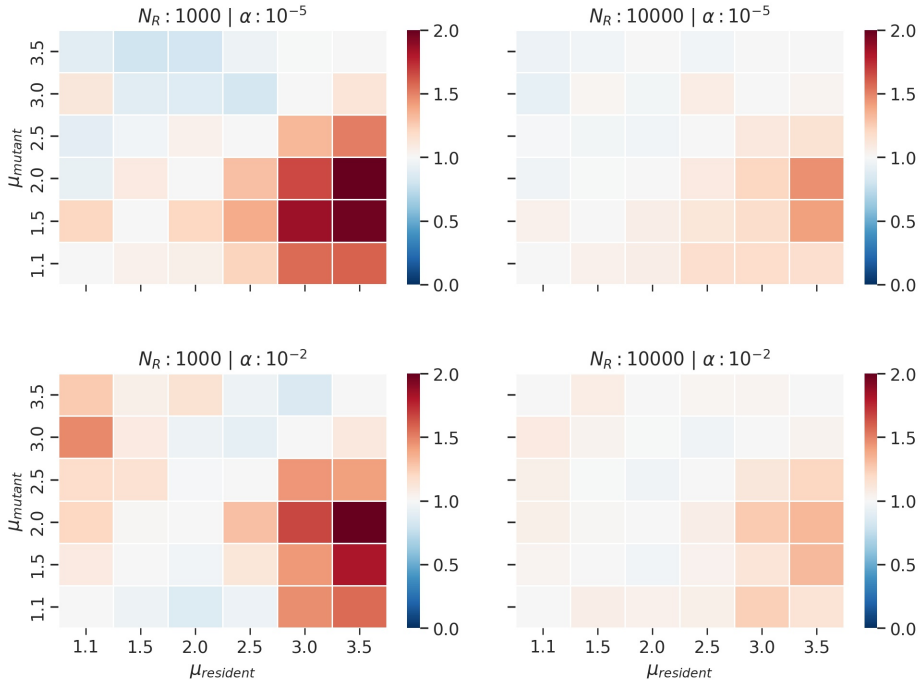

Fig.S11: Mean estimates of invasion index for groups of size 50, different levels of resource density (N_R) and social learning (α) over 500 simulations. Index values greater than 1 imply that the mutant μ will be over to invade the resident μ and are represented by red hues.

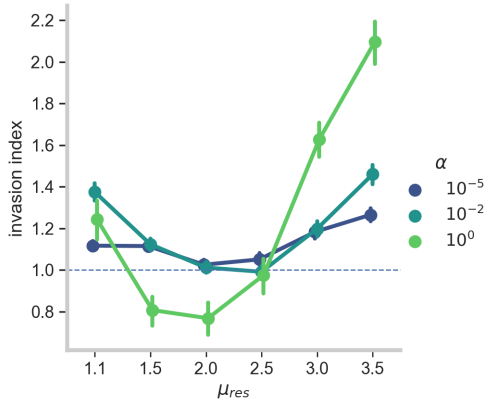

Fig.S12: Overall mean estimates of invasion index for all groups of size 10 and 50, different levels of resource density (N_R) and different μ_{mut}. Different colors indicate the three levels of social learning (α). This plot shows that on an average among all the different conditions, $\mu_{res} \approx 2$ is least likely to be invaded by other strategies.

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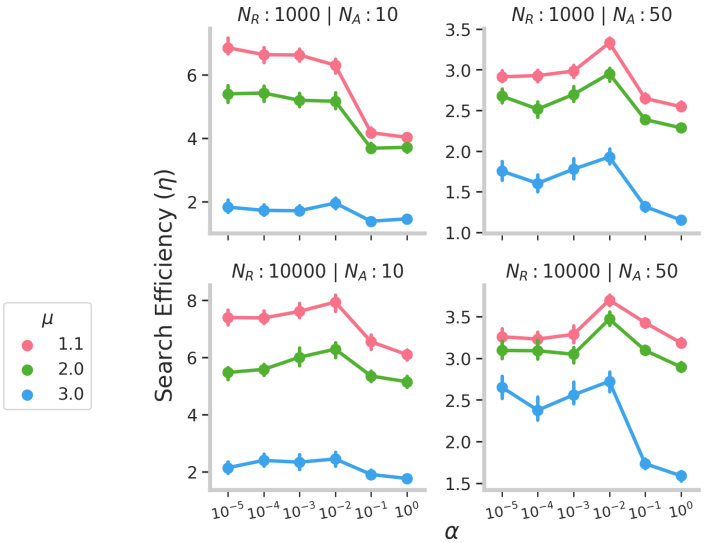

Fig.S13: Group search efficiency η for the ARS model as a function of social selectivity parameter α, Lévy exponent μ, resource density N_R. Error bars indicate 95% confidence intervals. Note the different Y-axes limits.