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From individual to collective foraging and their interplay: Efficiently balancing trade-offs in search processes

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From individual to collective foraging and their interplay: Efficiently balancing trade-offs in search processes

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by

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The dissertation of Ketika Garg, is approved, and it is acceptable in quality and form for publication.

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To *mumma*,
like much else, this is for and from you.

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Talks and Conferences

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(Invited talk) Individual and social learning in collective search
Feb 2022; MPI-Berlin (virtual)

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(**Talk presented**) Foraging in the Virtual Himalayas: Intrinsic and Extrinsic Factors in Search
July 2020; 42$^{\text{nd}}$ Annual Conference of the Cognitive Science Society.

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Abstract

Search is a fundamental process that illustrates adaptive, goal-directed behavior across multiple scales and contexts: from organisms foraging for food independently or collectively, to networked teams searching for solutions to a problem. Efficient search in an environment or a problem-space requires managing a primary trade-off between exploiting available options, resources, or information and exploring for more. In collaboration with other co-authors, I present experimental and modeling work on how individuals and groups can balance this and other related trade-offs to search efficiently under different constraints, and the interplay between individual and group search trade-offs and behavior.

Using a virtual game environment with ecologically-valid constraints, I show that individual humans can efficiently search a previously unknown environment by balancing explorative and exploitative search modes and flexibly adapting this balance based on their task and cognitive constraints (Chapter 2). However, as part of a group, individuals are faced with another essential trade-off: whether to use social information to find resources or search independently. Using an agent-based model of collective foraging, I show that selective use of social information and high levels of independent, explorative search can allow groups to simultaneously take advantage of collective information while maintaining exploration for new resources (Chapter 3). Further, I show that groups may not always evolve to be composed of explorers that maximize a group's efficiency and that competition for resources can result in less efficient groups composed of both explorers and exploiters. I further demonstrate how simple heuristics like area-restricted search can benefit explorers and maximize both individual and group search efficiencies (Chapter 4). Finally, a group's ability to search for resources or solutions over a problem-space can also be affected by patterns of social interactions between individuals. By simulating central-place foraging in early humans, I show that their movement patterns could have led them to interact in ways that created social networks efficient at exchanging information and balancing collective exploration and exploitation of solutions (Chapter 5). Taken together, these results suggest that efficient search in individuals and groups is driven by an adaptive balance between exploration and exploitation, which is further affected by their physical and social environments. It also sheds light on the interplay between individual and collective search that has implications for topics ranging from decision-making, animal foraging, organizational learning to cultural evolution.

This dissertation, *From individual to collective foraging and their interplay: efficiently balancing trade-offs in search processes*, is submitted by Ketika Garg in the summer of 2022 in partial fulfillment of the degree Doctor of Philosophy in Cognitive and Information Sciences at the University of California, Merced, under the guidance of Prof. Christopher T. Kello.

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Chapter 1

Introduction

Foraging to find relevant resources like food, shelter, and conspecifics is a fundamental goal-directed behavior practiced by all living organisms, ranging from relatively ‘simple’ bacteria to cognitively-complex humans. Foraging research occupies a special place in behavioral sciences that can link questions that scale up from cognition and decisions at the level of an individual organism to the collective and population-level phenomena. It also presents a unique perspective on understanding the effect of physical and social environments and their interplay on the individual- and group-level decisions and behavior. In addition, since most of human evolutionary history has been in foraging economies (Alden Smith, 1983), foraging behavior could likely have had significant consequences on our cognitive, social and cultural evolution, and by studying foraging, we can shed light on our evolutionary trajectory. While foraging is an important behavior to study, it also presents a view into general and inter-related phenomena like search, decision-making, problem-solving, and collective systems.

However, to efficiently forage for relevant resources, both individuals and groups need to manage certain fundamental trade-offs in their foraging decisions and behaviors. One of the most ingrained trade-off is between exploiting known opportunities, information or resources, and exploring for new, previously undiscovered information or resources, and how foragers balance this trade-off can have significant consequences for their search efficiencies. Further, the optimal balance between exploration and exploitation may change depending upon the physical and social environmental, and task constraints. In this chapter, I discuss the main theories of foraging, the different trade-offs that foragers face while searching independently and collectively, and how individual and collective foraging behaviors can affect each other. The studies presented in the dissertation build upon the theories discussed below and shows how efficient foraging and search balances the different trade-offs at both the individual and collective scales.

1.1 Theories of individual-level foraging

A primary, over-arching question in foraging theory is how a forager should search efficiently to minimize its costs and balance various trade-offs that arise due to conflicting costs and benefits of the many processes involved. In a hypothetical ideal world with no constraining factors like energy, time, or effort, the optimal search process would be the one that exhaustively explores every point in the search-space with maximum time, effort, and engagement. However, that is not the case in the real world, where extrinsic and intrinsic factors such as environmental structure, social groups, travel time, mental effort, and attention constrain foragers. These constraints frame various trade-offs like exploration vs. exploitation, speed vs. accuracy, etc. A constrained forager with limited time and energy would need to decide how to spend its time and energy exploiting already-found but diminishing resources with exploring new, un-depleted resources at a greater risk. The resource environment directly affects this balance between exploration and exploitation (for example, travel time between patches, and the richness of patches).

Apart from extrinsic constraints of the environment or search-space, a forager may be constrained intrinsically, too. Brains have limited capacity to process and integrate information simultaneously and effectively, and attending to a large amount of information might decrease performance quality. *Attention* is a limited resource, and limited attention results in a restriction in the amount of information the brain can process at a given time. Many studies have investigated the effects of limited attention on animal and human target-selection decisions in visual foraging tasks (Dukas, 2004). Similarly, integrating and processing information requires cognitive effort, and previous studies have shown that animal and human decision-making is influenced by the costs of mental effort (Kool and Botvinick, 2018). Such constraints can underline other similar trade-offs, such as between speed and accuracy or speed and perception.

As I outline below, most of the literature around this question is based mainly upon two theories that address this problem from different but related angles. *Optimal Foraging Theory (OFT)* focuses on the decisions that an optimal forager should make regarding choices like which resource option to select from many, when to leave a diminishing food patch, and which location to choose to settle a home-base. The bedrock principle that this theory builds upon is that optimal foraging should maximize a given currency (such as energy) and modulate its decisions based on the environmental constraints. For example, using the *Marginal Value Theorem* (Charnov and others, 1976), it predicts that an optimal forager should stop exploiting a patch when the rate of energy intake at the current patch falls below the expected average intake rate of the environment. It predicts that an optimal forager should switch from exploiting a patch to exploring for more patches when the rate of finding food from a patch is equal to the average expected gain rate from the environment, inclusive of the travel time between patches. In other words, when the resource environment is rich, the optimal strategy would favor shorter exploitative bouts. However, when travel time is significant in sparse environments, foragers should allocate more time and accuracy to exploit a patch. In addition to time, thorough exploitation of resources can require effort, and depending upon the forager's state, they may adjust the amount of effort they invest in maintaining the accuracy of their decisions even with a reduced amount of time available (de Froment et al., 2014).

Another perspective is offered by the *random-walk theory*, which follows the principle of OFT and predicts *how* foragers should optimally search for resources. While OFT assumes that foragers have complete knowledge of their environment - resource distribution, travel times, etc., the random-walk theory assumes that foragers have no prior information about the environment structure. Many empirical (Bartumeus et al., 2003; Boyer et al., 2004; Brown et al., 2007; Da Luz et al., 2016; Focardi et al., 2009; Namboodiri et al., 2016; Raichien et al., 2014; Reynolds and Frye, 2007) and theoretical studies (Bartumeus et al., 2014; Viswanathan et al., 1996) have shown that a special class of random walks, *Lévy Walks* can represent optimal search patterns that minimizes search costs and maximizes resource intake. Lévy walks (LW) are comprised of frequent short movements interspersed with rare, longer movements whose probability is governed by a power-law exponent, μ. In specific, the probability of observing a given path length is inversely proportional to the length, $P(l) \sim l_j^{-\mu}$ and the length of step j is l_j, the power law exponent μ is bounded, $1 < \mu \leq 3$, and the movement steps refer to the distance traveled between two consecutive pauses or turns.

The value of μ can modulate the exploration-exploitation trade-off based on the environmental constraints. For example, when resources are non-destructive or patchy, $\mu \approx 2$ can balance revisiting or exploiting nearby targets (re-sampling areas), and leaving a visited area to explore for new targets. But when resources are destructive and it is disadvantageous to backtrack and re-sample an area, $\mu \to 1$ can increase explorative search bouts and thereby increase search efficiency. Lévy-like patterns can arise from decisions motivated by optimal foraging theory, too. For example, when resources are plentiful but far apart, it would be optimal to spend a longer time exploiting a patch. This behavior would inevitably create a distribution of path lengths leaning on short movements and quick turns (or $\mu \to 3$). However, in the lack of prior knowledge about the environment, a search pattern with $\mu \approx 2$ might be generally beneficial due to the balance between movement bouts of high speed can help cover (or explore) large distances quickly but at the cost of low detection (or exploitation) of resources with slower bouts with more focused and thorough exploitation can give rise to $\mu \approx 2$ (Bénichou et al., 2011; Campos et al., 2012).

In Chapter 2 (*Efficient Lévy walks in human foraging*), within the framework of these theories, I present experimental data on human foraging in ecologically-valid virtual environments to shed light on how humans move and forage in realistic environments and balance these various trade-offs in the face of extrinsic and intrinsic constraints. Our results show the presence of $\mu \approx 2$ in efficient search behavior that balanced exploitative and explorative modes of search, irrespective of task constraints.

However, we also found that efficient foragers built upon these patterns and modified their search behavior to adapt to contextual and cognitive constraints. Further, our results advocate integrating physics-based foraging theories with more cognitive approaches to explain how cognition builds on more basic search processes to guide foraging behaviors in humans and other complex organisms.

1.2 Transitioning to collective foraging

Individual foraging represents only a section of real-world foraging practices where many animals are social and engage in *collective foraging*. Individual foraging can represent a simpler approximation of a more complex problem: it assumes a single active 'particle' with internal properties. It interacts with its immediate environment, akin to an ideal gas approximation that does not consider interactions between random gas particles. A more realistic scenario has multiple active, moving 'particles' that *interact* with each other. In collective foraging, the extrinsic constraints that affect individual search behavior would now include the social environment in addition to the physical one. In other words, search behavior could be affected by how group members interact with each other and others' search strategies. For instance, based on MVT, we can predict that the optimal time to exploit a patch before switching to exploration for new patches might decrease if many agents collectively exploit a patch and deplete it faster. Furthermore, individual search strategies and their interaction patterns can affect group-level performance, often in non-linear ways.

In collective foraging systems, at the level of individual foragers, an additional trade-off arises between independently searching and using social information to find resources. Information about the environment or the resources present can be searched independently by an individual searcher, but when in a group, information can be gained or learned from group members, too. Social information or social learning can reduce costs and risks associated with searching independently and facilitate information pooling. However, excessive use of social information can decrease group-level discovery rate for new resources, amplify errors, cause informational cascades (Bikhchandani et al., 1992) and possibly have negative consequences for group adaptability. While collective foraging is directly related to understanding the foraging behavior of various natural systems, it also represents a general problem of collective or distributed search that underlines seemingly unrelated topics ranging from problem-solving, organizational learning, to cultural evolution where individuals can learn from others.

Some of the most common examples of collective foraging come from eusocial insects, that share information about profitable food sources through various mechanisms such as honey-bee waggle dances (Seeley and Buhrman, 1999; Von Frisch, 2013) and pheromone trails in ants (Dornhaus and Chittka, 2004; Hölldobler et al., 1990). These information-sharing or social learning mechanisms can also inadvertently trigger negative consequences of social information and learning. For example, pheromones deposited by ants en route to resources can serve as social cues for others to find food that can get amplified by positive-feedback loops and increase recruitment to the food resource. However, such amplification can reduce group-level exploration for new resources and thus, reduce the flexibility to quickly respond to another potentially higher-quality resource (Beckers et al., 1990). Further, the physical and social environment affects the optimal independent search and social learning strategies. For example, some studies have shown that collective foragers like ants and bees pay more information to social cues *when* acquiring personal information is difficult, and time costs of exploration are high (Grüter and Leadbeater, 2014). The benefits of social learning also increase in spatially auto-correlated or clustered resource environments (Luthra and Todd, 2021), and decrease when the problem-space is rugged and not correlated, such that the probability of finding solutions in the vicinity of previously found solutions is low (Sloman et al., 2021). Similarly, the social environment can affect how individuals should independently search and socially learn from others to maximize group efficiency. For instance, if the groups are large with many social learners, the benefits of social learning might further decrease due to excessive social amplification, and it would be advantageous for individuals to be selective in social learning. In addition, highly explorative strategies in groups that allow individuals to decrease overlap in search-space with others might help groups escape from being stuck in local minima and increase group performance and adaptability (Freeman and

Huang, 2014; Hong and Page, 2004; Winterhalder, 1986).

In Chapter 3 (*Individual exploration and selective social learning: balancing exploration-exploitation trade-offs in collective foraging*), I present a model of collective foraging that studies the interplay of the two fundamental trade-offs: (a) whether to use social information to find resources or to independently search, and (b) whether to independently explore distant areas or exploit near previously found resources. 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. We found that selective social learning and high levels of independent exploration can modulate the disadvantages of excessive social learning and give rise to an optimal combination of exploration and exploitation at the group-level.

However, optimal strategies at the group-level may not be evolutionarily stable at the individual-level. There is no guarantee that evolution through natural selection will always lead to an increase in population fitness. In many settings, where the fitness of a strategy is dependent on another strategy, the strategies selected over time can shape the evolutionary fitness landscape and result in frequency-dependent selection (Nowak and Sigmund, 2004). Further, previous studies have shown that indiscriminate social learning can diminish population fitness instead of increasing it (Rogers, 1988).

In Chapter 4 (*Evolutionary dynamics of independent search strategies in collective foraging*), I present an extended version of the collective foraging model to study the evolution of individual search strategies under different levels of social learning. In this chapter, we asked how the evolution of different search strategies is affected by their physical and social environment; and whether the optimal individual-level search strategies observed in the previous chapter are evolutionarily stable or not. We found that highly explorative search strategies are not evolutionarily stable, especially when the explorer's share is lower than that of exploiters (for example, in scarce resource conditions). Instead, we found that under these conditions, the evolved groups are composed of mixed strategies with differing proportions of explorers and exploiters. We further studied the effect of the evolved search strategies on group efficiency, and found that groups with rare explorers are not as efficient as those with more frequent explorers. We also modified the payoffs from exploratory strategies by adding a simple heuristic (i.e., area-restricted search) that allows them to gain a larger share of a resource patch and prevent being replaced by exploitative strategies.

1.3 From individuals to networks

Sharing social information can affect individual movements and increase a group's foraging efficiency. However, how individuals move and encounter each other can affect how groups share information or the group's social network, too. We can define a network as a system of interacting individuals that communicate with each other, where the interactions between the individuals is used to transfer information, and the structure of the network influences how the information flows on the network (Pinter-Wollman et al., 2011). Network structures and information transmission can have significant effects on how quickly some stimuli/information spreads across the group, the speed with which a group reaches a decision.

Network structures can modulate explore-exploit trade-offs in collective search, too, and affect its overall search dynamics Fang et al. (2010); Lazer and Friedman (2007). Too much connectivity within a network would lead to a rapid exchange of information and decrease the exploration for new solutions. Conversely, very sparsely connected networks will prevent the social group from accessing the solutions obtained by others. As a solution to this trade-off, some studies have suggested that small-world network topologies that have well-connected sub-groups within a sparsely connected, more extensive network can balance exploration for new solutions and exploitation of the solutions already found (Derex and Boyd, 2016b). In the context of humans and on longer timescales, social network structures and efficient information exchange can have important consequences for social structures and cultural systems.

Efficient information exchange in social networks of prehistoric and contemporary hunter-gatherer social networks has been suggested to be necessary for technological evolution, cultural transmission, and complexity (Migliano et al., 2017; Romano et al., 2020; Whallon, 2006). For most human early history, movement likely played a significant role in determining interaction patterns such as the frequency and strength of interactions and, thus, their social networks. In turn, movement and the spatial distribution patterns of prehistoric hunter-gatherers would have primarily depended upon movement driven by foraging and settlement decisions. As mentioned earlier, human foraging and movement patterns have been shown to follow optimal foraging decisions. Many studies on present-day hunter-gatherers have demonstrated that the decisions of which food resource to harvest or which prey to capture can be driven by predictions from OFT (Alden Smith, 1983; Pacheco-Cobos et al., 2019; Winterhalder, 1981). However, hunter-gatherer movement patterns are not limited to foraging trips. Many hunter-gatherers are central-place foragers who conduct regular foraging trips from a home-base within a foraging radius and periodically move their home-base to different locations. A few studies have shown that the decision to move the home-base can be driven by OFT, too (Venkataraman et al., 2017).

In Chapter 5 (*Modeling hunter-gatherer social networks from individual-level foraging and movement patterns*), I present an agent-based model that uses optimal foraging rules to operationalize central-place foraging and movement, and tests the resultant patterns of interaction for their efficiency to exchange information. We found that heterogeneous environmental conditions could have led foraging groups to stay localized in an area frequently and promoted long-distance residential movements that could have connected dense clusters of bands to form a partially-connected regional network. We further found that such a network structure could have been efficient for local and global information exchange. In other words, it could have a balanced exchange of information, cultural traits, and artifacts within sub-groups alongside sharing at the regional scale. Such efficient information exchange would not have only made collective foraging efficient, but it would have had a significant effect on our species' ability to *collectively search* for solutions on many complex problem-spaces, and changed our evolutionary trajectory.

Chapter 2

Efficient Lévy Walks in Virtual Human Foraging

2.1 Preface

I begin by presenting a chapter on individual-level foraging where we conducted an experimental foraging task with human participants in an ecologically-valid virtual environment. The study shows that efficient foraging movements resemble theoretically optimum Lévy-walk patterns that balance long, explorative search bouts with short, exploitative ones, irrespective of the shape of their overall search trajectories. In addition to movement-based search, we also analyze how efficient foragers utilize the time spent between moving by carefully scanning their environment to search for resources and plan their future movements. Altogether, we demonstrate that humans can forage efficiently by arranging and adjusting Lévy-distributed search activities in response to environmental and task constraints.

2.2 Introduction

Human intelligence appears to have an evolutionary basis, at least in part, in foraging and other search activities of our hunter-gatherer ancestors (Kuhn et al., 2016; Rosati, 2017). Presumably, survival depended not only on our ability to search effectively but also to flexibly adapt to goals and constraints as they arise and change. Goals and constraints are influenced by environmental conditions–such as terrain features, energy expenditure, and distribution of food and other resources–and by individual and social factors, such as the need to return to home and participate in social activities (Pacheco-Cobos et al., 2019). Efficient foragers need to manage the trade-offs that these conditions and factors are likely to present. Our ancestors may have used and honed their cognitive capacities for managing trade-offs and other foraging functions. However, less sophisticated strategies can be effectively deployed when knowledge or cognitive capacities are lacking. In particular, random search patterns can be efficient without requiring much memory, planning, or decision-making.

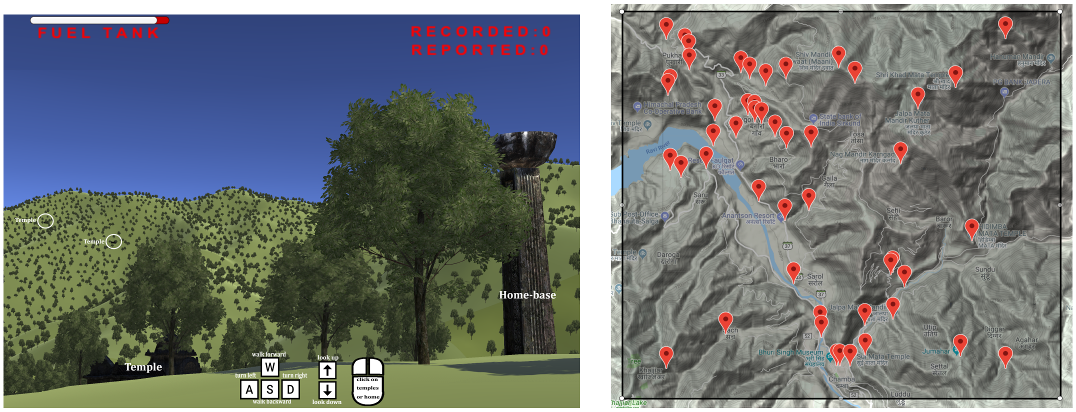


Figure 2.1: Game Environment. **Left:** An illustrative view of the virtual foraging game (key and mouse icons not shown during game play). Keys were used to move forward or backward (‘w’ or ‘s’), turn left or right (‘a’ or ‘d’), or tilt the view (‘up’ or ‘down’). The mouse was used to click on temples or the home-base. The ’fuel tank’ showed the current energy remaining, ‘reported’ showed a running count of temples scored, and ‘recorded’ showed the current number of temples found but not yet reported to home-base (home-range condition only). **Right:** Distribution of selected temples in the Google Maps (Maps data ©2018) view of the Himalayan terrain.

In random search, movement displacements and pauses between movements can vary stochastically to effectively explore the environment (Bartumeus, 2007; Bartumeus et al., 2016b; Sims et al., 2008; Viswanathan et al., 1999). Efficient random search has been formalized in terms of *Lévy walks* in which displacement sizes are drawn from a heavy-tailed distribution, and the probability of observing a given displacement is inversely proportional to its length(l), $P(l) \sim l^{-\mu}$; $1 < \mu \leq 3$. The Lévy exponent $\mu = 2$ generates superdiffusive search trajectories when directions are chosen at random at every step. Lévy walks generate displacements over a large range of scales that allow efficient sampling of an uncertain environment (Bartumeus et al., 2003). Such trajectories can balance extensive exploration of the search space that reduces the chances of revisiting areas with intensive coverage of immediate surroundings, as is beneficial when resources are scarce and their locations unknown. Studies have reported evidence for Lévy-like foraging in many different species, including humans (Boyer et al., 2012). For example, Lévy walks were observed in hunter-gatherer tribes in the Dobe Ju/'Ohoansi population (Brown et al., 2007), and the Hadza of Tanzania (Raichien et al., 2014). The pauses between movements can have effects on movement patterns (Bartumeus and Levin, 2008; Kölzsch et al., 2015; Kramer and McLaughlin, 2001), and they can be essential for resting, resource detection, and visual scanning. The lengths of pause durations can also be distributed akin to Lévy walks (Bazazi et al., 2012; Grove et al., 2010; Reynolds, 2015), which we return to later.

Lévy walks increase search efficiency under the assumption of perfect, effortless detection of sparse resources. However, real perceptual systems are less than perfect and perceptual accuracy requires effort and concentration. For instance, the proportion of time and effort spent on relatively intensive search activities can increase with the difficulty of resource detection (Bond and Kamil, 2006; de Froment et al., 2014; Spaethe et al., 2006). Furthermore, the difficulty of resource detection can increase with movement speed (Campos et al., 2012) as a form of speed/accuracy trade-off (Bogacz et al., 2006; Chittka et al., 2009). More generally, attention is a limited resource and must be selectively allocated based on prevalent foraging conditions (Chittka and Raine, 2006; Nityananda and Chittka, 2015; Zhang et al., 2018). Thus, the flexibility in search strategies necessary to adapt to diverse environments might stem from the combination of locomotive and perceptual processes (Viswanathan et al., 2011), and a full understanding of foraging behavior requires an integration of the two. Despite the interdependence of locomotion and perception, they need not be affected by similar constraints. For instance, locomotion is inherently constrained by the landscape and energy expenditure (Ross and Winterhalder, 2015; Wilson et al., 2012), whereas perceptual accuracy is constrained by time and ability to concentrate (de Froment et al., 2014).

The roles of perception and attention highlight how foraging is a *multiscale* process: relatively local perceptual and attentional processes unfold on shorter timescales, and these processes must be coordinated with movement and decision-making processes that unfold over a broader range of temporal and spatial scales (Gameiro et al., 2017; LaScala-Gruenewald et al., 2019). Previous studies illustrate how foraging decisions in humans and other complex organisms are guided to minimize time and energy expenditure. However, decision-making is itself a process that primarily expends time and effort, and energy to a lesser degree (Mugan and MacIver, 2020). Despite this rationale, there is little research on how time and energy are managed to make foraging decisions and movements. This research question is challenging to address in natural foraging because of the lack of experimental control and inability to measure behavior at a resolution needed for data on perceptual and decision-making processes. Some studies of human foraging have used simplified tasks and games to run controlled experiments (Kalff and Hills, 2006; Kerster et al., 2016b; Martínez-García et al., 2017), but these studies mostly lack essential features like energy costs (Kamil et al., 1987; Korn and Bach, 2018) and multiscale interactions between perception, movement, and decision-making that are the bases of efficient foraging.

2.3 Experiment

We designed a virtual environment to study human foraging in a natural setting that engages multiscale processing while also affording experimental control and a range of detailed measurements (links to the game can be found in Methods). We aimed to investigate the extent to which efficient human foraging is founded on basic search processes and how search processes are augmented by decision-making based on trade-offs between effort expended on movement versus planning and perception.

The primary trade-off occurs between local versus non-local search processes, i.e., those driven by sensory activity versus locomotive activity, akin to the trade-off between intra-patch versus inter-patch foraging (Pacheco-Cobos et al., 2019; Zollner and Lima, 1999). The present study examines how this trade-off is managed for efficient foraging under different task conditions.

We replicated a region in the foothills of the Himalayas using Google Maps and the Unity 3D game engine (Fig 2.1). The region has several ancient temples whose locations we used to model the distribution of resources to be foraged for. These temples are spatially distributed according to human on-foot movement patterns and various socio-cultural and environmental factors (Zurick et al., 2014). Historically, they may have served as waypoints for journeys of nomadic tribes of the region (Kaushal, 2001). The region is heterogeneous in terms of terrain elevation and visibility, thereby invoking naturally complex decision-making about energy expenditure for locomotion (Wilson et al., 2012) aimed at exploration versus reaching better vantage points for visual search (Mugan and MacIver, 2020). Players foraged by moving through the environment at a constant human-scale velocity, and energy was expended as an empirically-based function of change in elevation (Minetti et al., 2002) (See Methods). Velocity was in the upper range of human athletic ability to increase the area that could be searched per unit time.

Our virtual foraging game allowed us to examine the behaviors of more versus less efficient human foragers, as gauged by the number of temples found (all players started in the same location with the same energy budget). We also tested for adaptive behavior, i.e. efficient responsiveness to task and environmental constraints, by manipulating the need to return to a home base, i.e. central-place foraging (Reynolds, 2008). This constraint is natural and variable in real-world conditions which suggests that humans and other organisms may have evolved to adjust to central-place variability. The foraging game also elicited the coordination of perceptual search with locomotive search in a relatively natural way. While players did not expend actual physical energy to play the game, they had to decide when and where to look or move to locate resources based on a simulation of the main functional constraints that apply in real human foraging.

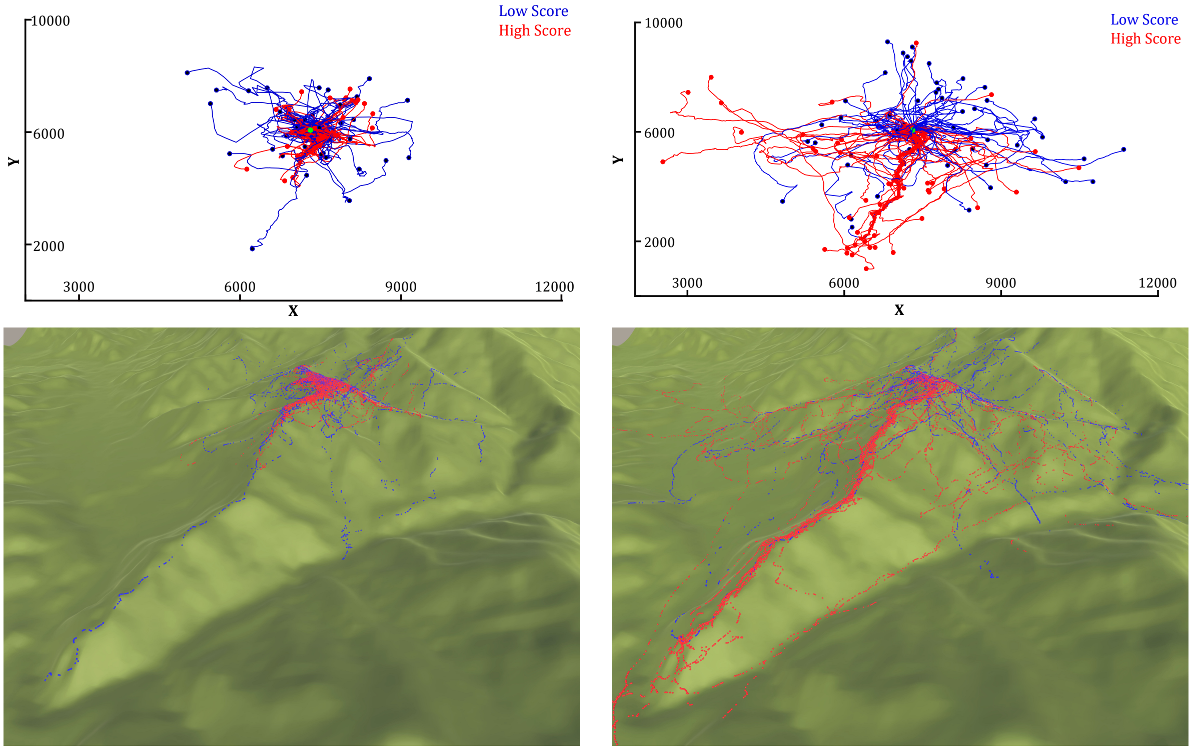


Figure 2.2: All search trajectories plotted for home-range players (**Left**) and free-range players (**Right**), in a 2D plane (**Top**) and the full 3D terrain (**Bottom**). Trajectories for low versus high scorers colored separately (blue versus red). The XY coordinates are in meters.

Each participant played individually, and each player started on top of a hill where a tower was placed as a home base. The hill was roughly in the middle of a 5x5 kilometer terrain map of the Himalayas that contained 49 temples registered in Google Earth (Fig 2.1). We populated the hilly terrain with scattered trees that made temples challenging to see from a distance due to occlusion and misidentification. In the *home-range* condition, players needed to click on the tower to score any temples they acquired up to that point. The players did not need to be next to the home-base to click on it, they could do so from a distance within close vicinity. In the *free-range* condition, temples were scored immediately when acquired, and players did not need

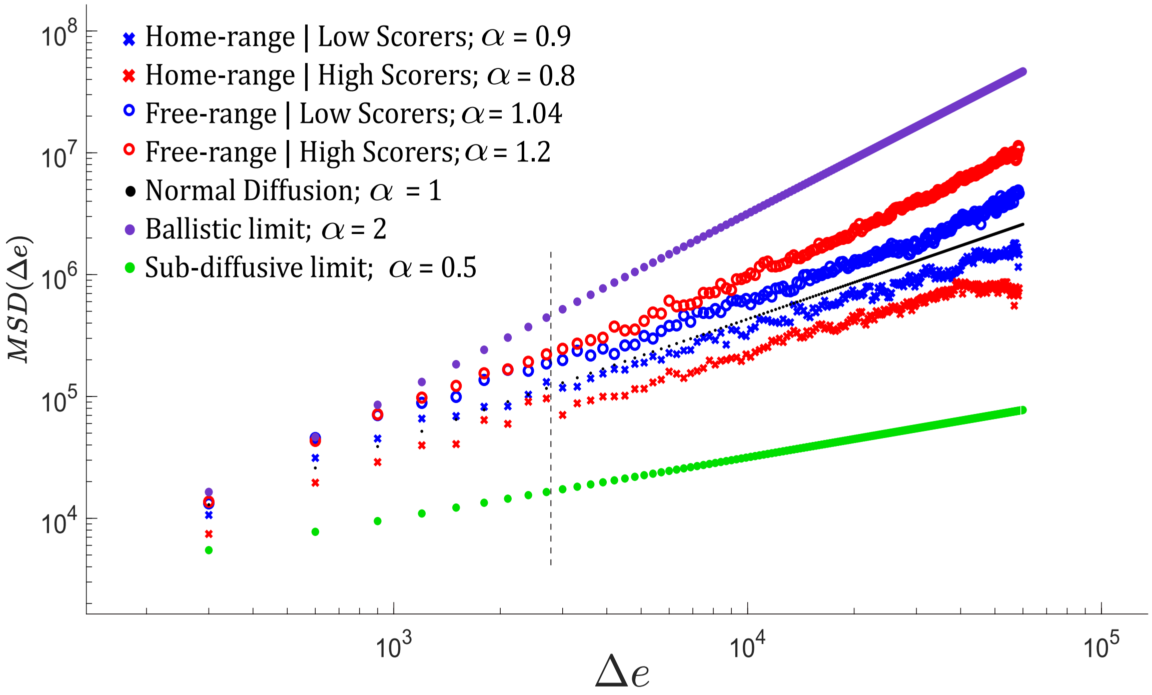


Figure 2.3: Mean Squared Displacement as a function of energy expended for the ensemble of trajectories in home-range and free-range conditions, separated by low (blue) and high (red) scorers. Functions are also divided into local (left) and non-local (right) scales by the vertical dashed black line, and anchors of normal diffusion and ballistic and sub-diffusive limits are shown for comparison.

to return to the home-base. The game ended only after the energy budget was depleted and the players were awarded 50 cents for finishing the game and an additional 20 cents for each temple scored. Only movements over the landscape cost energy, forward and backward, and players were given an energy budget that enabled them to approach the edges of the game space without reaching them. Energy expenditure was constant for flat and downhill movement and increased linearly with the grade of uphill movement. Given a constant velocity and limited energy budget, the duration of the game was affected by the rate of energy expenditure, for example, more uphill movement increased the rate of energy loss and decreased the total play time.

In typical foraging models, foragers expend energy to move near enough to a resource to perceive it and then move additionally to access it. This additional movement is irrelevant for our purposes, given that the search process is complete at the moment of perceptual detection. To avoid wasting time and energy to walk close enough to physical resources to touch them, players obtained "informational" resources by simply clicking on them upon visual detection.

This informational mode enabled us to measure the perceptual component of foraging, as expressed in reorientations used to scan the landscape for resources visually. It also highlighted the trade-off between visual scanning via reorientations that searched without energy expenditure versus locomotion that brought distant hillsides and other unexplored areas into view. Visual scanning cost time but not energy, whereas locomotion cost both time and energy. Players could increase their play time by taking longer pauses at the cost of time and opportunity. Visual acquisition of resources was reflected in player scores but did not replenish energy levels and the goal was to record as many resources as possible, given a limited energy budget. This goal is based on typical foraging models, where foraging efficiency is defined as maximizing resources as a function of energy integrated over time (Ydenberg et al., 1994).

The game was hosted on Amazon's Mechanical Turk, and 200 unique participants completed the game without technical or other issues–100 in the free-range condition, and 100 in the home-range condition. Players took an average of 12 minutes to expend their energy budget, and the mean performance for the two conditions was the same at 7.0 temples scored. To assess how the efficiency in foraging behavior interacted with the home-range constraint, we further divided the players based on their scores using a median split, such that the players scoring less and more than the median of 4 were labeled as 'low-scorers' and 'high-scorers' respectively. We tested how this median split interacted with the manipulation of home base, and we show that bivariate results are consistent with the underlying continuous relationships between measures of foraging and score.

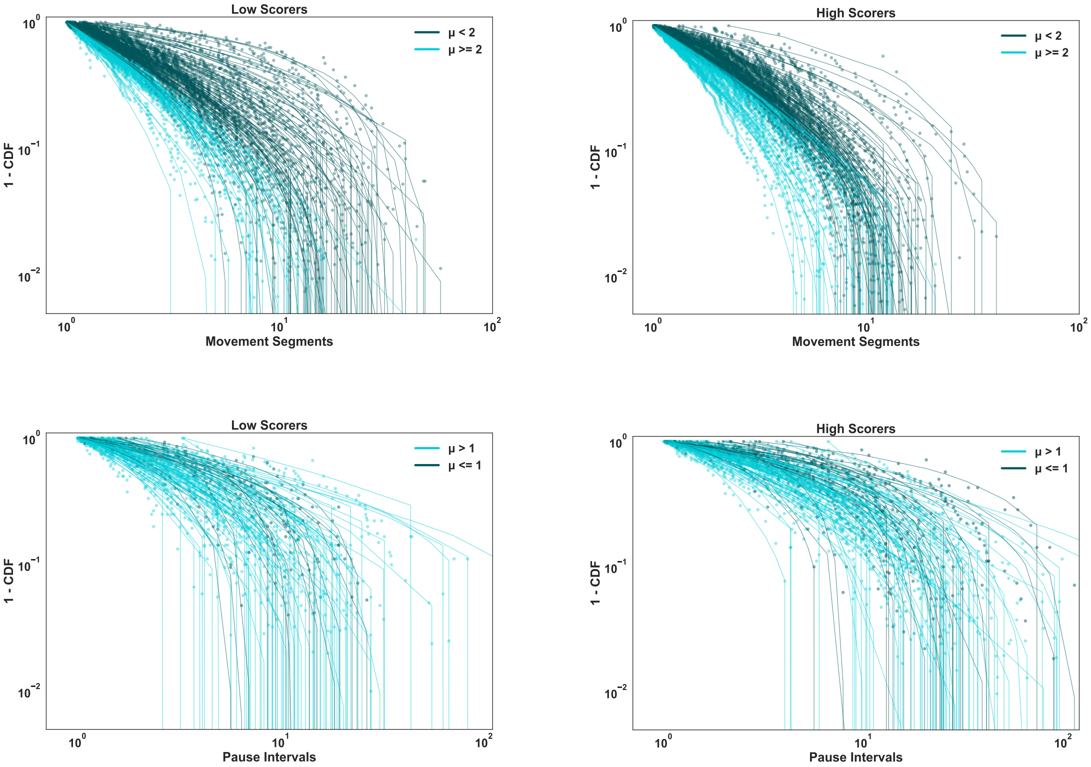


Figure 2.4: Complementary Cumulative Distribution Function (CCDF or 1 - CDF) for movement segments (**top row**) and pause intervals (**bottom row**) for all low scorers and high scorers. The points represent the empirical data and solid lines show the corresponding truncated power-law fits (using Eqn(2.2) where μ is the maximum likelihood estimate for a given empirical distribution, and $x_{\min}$ is set to 1 sec). Lines are colored to show the boundaries of $\mu = 2$ for movement segments and $\mu = 1$ for pause intervals.

2.4 Results

2.4.1 Efficient foraging was more adaptive in response to home-range constraints

All individual search trajectories are shown in Fig 2.2 with and without the terrain as the backdrop (top versus bottom) for home-range versus free-range players (left versus right). Before proceeding with analyses, we can observe that foragers generally adapted their movements to task demands in that trajectories were less spread out in the home-range condition. Moreover, this adaptation appears to be more pronounced for high scorers in that the red trajectories appear to be less spread out than blue trajectories in the home-range condition. In contrast, the opposite is true in the free-range condition.

To quantify and test these apparent differences, we used diffusion analysis to measure the degree of spatial dispersion of search trajectories. Diffusion analysis is based on change in mean squared displacement (MSD) over time (T), where $MSD \approx T^{\alpha}$ and $\alpha = 1$ corresponds to a random Brownian walk. Subdiffusive ($\alpha < 1$) and superdiffusive ($\alpha > 1$) trajectories indicate anomalous diffusion, where the MSD can either grow slower or faster than expected by a random walk. MSD is usually computed as a function of time, but we computed it as a function of energy expenditure, which is more directly linked with movement dispersal in our game as in real environments.

MSD functions were similar across conditions at local scales (see upcoming segment analyses), but they diverged at longer scales. We calculated MSD from an ensemble average (see Methods) for each condition over all scales to estimate the degrees to which players ranged farther or less far compared with the normal diffusion baseline of $\alpha = 1$ (Fig 2.3). We simulated a random walk to confirm that the effect of varying slopes on energy expenditure did not cause a bias away from the baseline of regular diffusion.

We also calculated MSD for every trajectory separately (Fig 2.5) and found that players were significantly superdiffusive in the free-range condition ($\overline{\alpha} = 1.3$, one-sample *t-test*: $t = 7.8$, *df* $= 99$, $p < 0.001$), and significantly subdiffusive in the home-range condition ($\overline{\alpha} = 0.86$, one-sample *t-test*: $t = -3.1$, *df* $= 99$, $p = 0.002$). Moreover, the effect of home-range was exaggerated for high versus low scorers as evidenced by a significant interaction between home-range condition and high/low scorers, $F(1, 196) = 11.5$, $p < 0.001$. We calculated F statistics using two-way (home condition x search efficiency) ANOVA and diffusion exponent estimates α for each player as the dependent variable. Fig 2.6 shows the mean α values for each condition separated by low versus high scorers. The MSD results confirm that players adapted their overall search trajectories to range farther in the free-range condition, and this adaptation was greater for high scorers.

The home-base served as a resource akin to a temple, i.e., a structure to be located. However, unlike temples, it was a non-destructive resource that players needed to return to, often repeatedly as players would go out on multiple excursions. The memory of the home-base's location presumably decays over time and distance (Bracis et al., 2015), so it is beneficial to restrain the dispersal distance when return trips are sufficiently valuable (Spencer, 2012). Efficient search in the home-range condition meant staying closer to the home base, which conserved energy and lessened the burden on memory by keeping the home base tower in view or not far from sight.

2.4.2 Efficient foraging followed Lévy walks regardless of home-range constraints

The diffusion analyses show how movement trajectories are distributed over long spatial and temporal scales to fit task constraints. Movement trajectories can also be analyzed segment by segment to examine the distribution of movement segments and the degree to which search activity is intensive versus extensive, i.e., relatively short versus long movement segments. The distributions of movement displacements play a role in the use of space and overall diffusion of foraging trajectories, but they can also reveal different patterns at a smaller scale that provide additional information about foraging processes (Bartumeus et al., 2016a).

We divided foraging trajectories into movement segments and pause intervals, where the former were defined as continuous intervals of forward or backward movement delineated by pauses in movement of any length. Pause intervals were continuous periods of standing still and turning without locomotion. We analyzed the frequency distributions of both kinds of segment distributions by fitting the parameters of several candidate models (see Methods for more details) using maximum-likelihood estimation (MLE). The best-fitting model was determined based on relative likelihoods using Akaike Information Criteria (AIC) and the Kolmogorov-Smirnov D goodness-of-fit metric. The candidate models tested were those most commonly examined in prior foraging studies, and each model was tested against the distribution of each participant.

AIC results showed the large majority of movement segment distributions, 81%, were best fit by the truncated power-law model. Therefore, we analyzed the best-fitting parameters of the truncated power-law (Eqn 2.2) for all trajectories to quantify and compare distributions across conditions (Fig 2.4). Estimated power-law exponents were almost entirely within the range of Lévy walks, $1 < \mu \leq 3$, and generally close to the theoretical optimum of two, as many studies have found (Reynolds et al., 2018; Sims et al., 2019; Viswanathan et al., 1999). $\mu \approx 2$ reflects a balance where shorter, energetically cheaper movements intensively search areas that are reached by longer, energetically more costly movements. The exponent also generates a broad range of step distributions that could help in a judicious sampling of the environment, especially under movement costs and uncertain conditions irrespective of how much space is covered (Bartumeus et al., 2003; Seuront and Stanley, 2014). The relationship between exponent and score (Fig 2.5) shows that foraging was generally most efficient near $\mu \approx 2$.

In line with Figure 2.5, we found that the mean estimated exponents (Fig 2.6)for high scorers ($\overline{\mu} = 1.89$) were reliably closer to optimal compared with low scorers ($\overline{\mu} = 1.70$), $F(1, 196) = 12.03$, $p = 0.05$, without any no reliable effect of home-range, $F(1, 196) = 0.15$, $p = 0.7$. Therefore, while the trajectory diffusion adapted to the home-range/free-range manipulation, the distribution of efficient movement segments resembled a Lévy walk regardless of task constraints. It is especially noteworthy that even the subdiffusive home-range trajectories were composed of Lévy-distributed movement segments. Lévy walks are mostly associated with superdiffusive trajectories and random heading directions that help avoid backtracking and reach unexplored areas. Home-range players were restricted to areas near the home base, but by not picking their headings at random, they were able to maximize their search efficiency within the limited space. Altogether, our results add to previous evidence for the prevalence of $\mu \approx 2$, even when the superdiffusive benefit of Lévy walks is nullified.

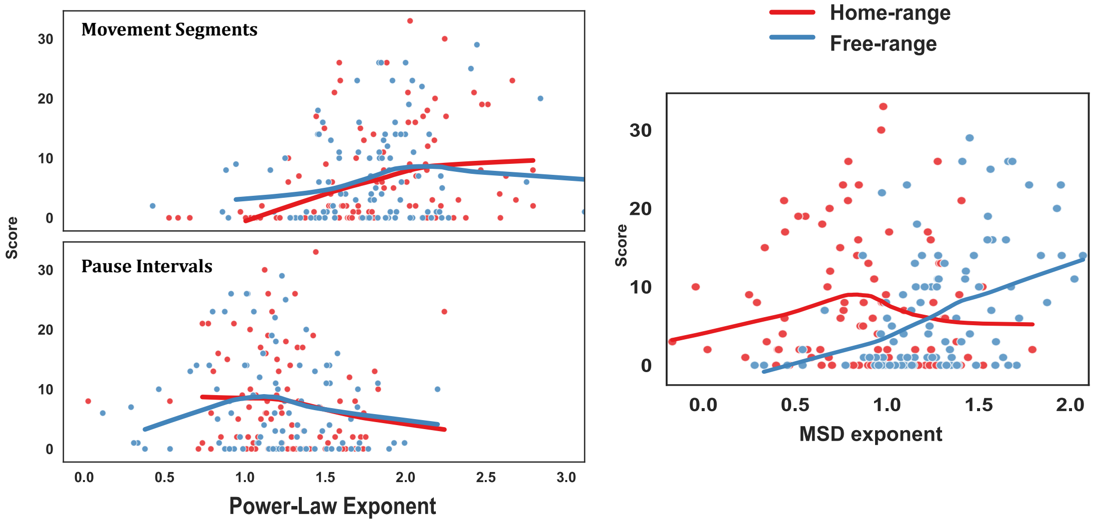


Figure 2.5: Individual scores as a function of truncated power-law exponents (**left**) for movement segments and pause intervals, and diffusion exponents (**right**) for home-range versus free-range foragers. The solid lines show the respective moving averages.

2.4.3 Efficient foraging benefited from concentrated bouts of perception and planning

Foraging in humans and other complex organisms involves perception, memory, planning, and decision-making processes that can be difficult to perform while moving (Kramer and McLaughlin, 2001), especially under challenging and uncertain conditions. Pauses between movements are sometimes attributed as “handling times” to retrieve and process resources in optimal foraging literature (Grove et al., 2010). In our experiment, pauses between movements were times when players, at the expense of time and effort, could plan their next moves or visually scan the environment for

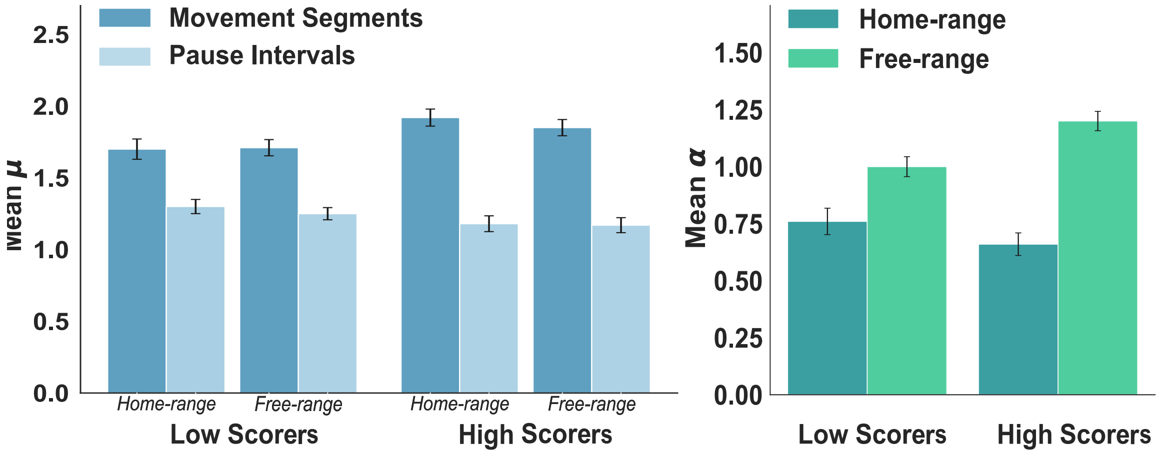


Figure 2.6: Mean truncated power-law exponents μ for movement segments and pause intervals (**left**), and mean diffusion exponents α (**right**) for home-range versus free-range foragers. Both measures shown separately for low versus high scorers, and error bars show standard errors of the means.

distant resources that may be difficult to discriminate from trees and other environmental features.

We first tested whether foraging-related activities were indeed engaged during pause intervals as assumed. We did not have access to direct evidence, but this hypothesis predicts that longer pauses should generally result in better performance due to the value of mental processing. Consistent with this prediction, we found moderately strong correlations between scores and summed pause intervals in both conditions, $r_{\text{home-range}} = 0.43$, $p < 0.001$ and $r_{\text{free-range}} = 0.60$, $p < 0.001$ (see Fig 2.7 (left)). We can infer that at least some time spent during pauses was used for visual scanning to detect temples or the home-base.

Intervals between foraging activities have been studied previously in sit-and-wait ambush predators, where waiting times are distributed according to a power-law (Wearmouth et al., 2014) analogous to the distribution of movement segments in Lévy walks (Reynolds et al., 2015). Similar to previous studies, power-law analyses of pause intervals showed that the majority of pause distributions, 76%, were best fit by one of the two power-law models, with 57% truncated Pareto and 19% pure Pareto. We found that μ parameter estimates for the truncated power-law model were closer to one than two (Fig 2.5), consistent with previous results showing evidence for power-law waiting time distributions with $\mu \approx 1$. Moreover, scores were generally highest when estimated exponents for pause intervals were close to $\mu \approx 1$, and exponents for high scorers were closer to one than for low scorers, $F(1, 179) = 3.8$, $p < 0.05$ (see Fig 2.6).

To understand why efficient pause intervals approached $\mu = 1$, we can compare this result with the corresponding analysis of movement segments where the exponent approached $\mu = 2$, which balances energetically costly longer movements with shorter, intensive clusters. For pauses, there is no such energetic cost (Raposo et al., 2003). To the contrary, relatively long, continuous pauses help to integrate visual information as the environment is scanned, integrate that information with prior knowledge, and consider possible plans for next foraging movements. Such mental processing requires sustained concentration that could be disrupted by too much task switching between movements and pause intervals, or too much difficulty in integrating information across the different viewpoints separated by movement segments. This explanation may be related to previous work showing that $\mu \approx 1$ can result from memory effects on task execution, such that humans perform an activity based on their past activity rate (Vazquez, 2007). Better players may be more aware of their activity rates and concentrate their mental efforts accordingly.

2.4.4 Efficient foraging traded more perception and planning for less exploration with the home-range constraint

We designed our foraging game with an explicit, empirically-based cost to foraging movements, but time and mental effort were inherent costs that players presumably took into account. They could favor exploratory movements over perception and planning, thereby expending energy in exchange for less time and effort, or they could invest more time and effort on careful visual scanning to detect trees or path planning to increase their search efficiency. The home-range constraint favored the latter because of the added energy costs of return trips (although players only needed to see and click the home base to score temples found, some return movement was often needed to bring it into view). The cost of these return trips is reflected in the diffusion results that showed more restricted, subdiffusive search areas with the home-range constraint. If one only takes movement-based search into account, then the need to return to home base should hinder performance because return movements expend the energy budget and thereby reduce the total amount of ground that can be covered.

On the contrary, as reported earlier, mean scores were nearly identical for home-range and free-range foraging. This surprising equivalency implies that home-range players could find almost as many temples as their counterparts without engaging in superdiffusive search. This result indicates that efficient foragers switched their foraging strategies in response to task constraints: Home-range players minimized ranging farther to avoid the movement costs of return trips, but they maintained performance by investing more time in planning or visual scanning. Analogously, optimal foraging models predict that the time spent by foragers in a patch should depend upon travel costs, among other factors (Stephens, 2008). Greater travel costs should increase the probability of exploiting a current location rather than exploring others. We predict that more significant travel costs in the home-range condition should lead players to exploit the area near the home-base by spending more time on planning and visual detection compared with free-range players (Bell, 1990).

In support of the predictions outlined above (see Fig 2.7 center), total time spent on visual processing was 52.47 seconds longer on average in the home-range versus free-range condition (one-tailed t-test: $t = 1.52$, $df = 198$, $p = 0.06$), and this effect was not reliably different for low versus high scorers. The extra pause time was apparently used for visual search/mental processing helpful to foraging efficiency, as evidenced by the correlation with scores reported earlier. To further corroborate that this extra time spent between movements in the home-range condition was used for visual search, we can find indirect evidence in the frequency and rate of reorientations (turns and head tilts while standing still) that are indicative of active visual scanning and effort.

As predicted, we found that the rate of reorientation was higher in the home-range condition (see Fig 2.7 (right)), $M = 0.18\,sec^{-1}$, than in the free-range condition, $M = 0.15\,sec^{-1}$ (one-tailed t-test: $t = 1.77$, $df = 198$, $p = 0.035$). Furthermore, high scorers ($M = 0.19\,sec^{-1}$) reoriented at a higher rate than low scorers ($t = 2.83$, $df = 198$, $p = 0.0025$, and high scorers adapted their reorientation rates somewhat more strongly to the home-range manipulation, $F(1, 196) = 2.81$, $p = 0.09$. These results indicate that the home-range constraint encouraged players to increase their investment in perception and planning, and better players made greater investments than worse players.

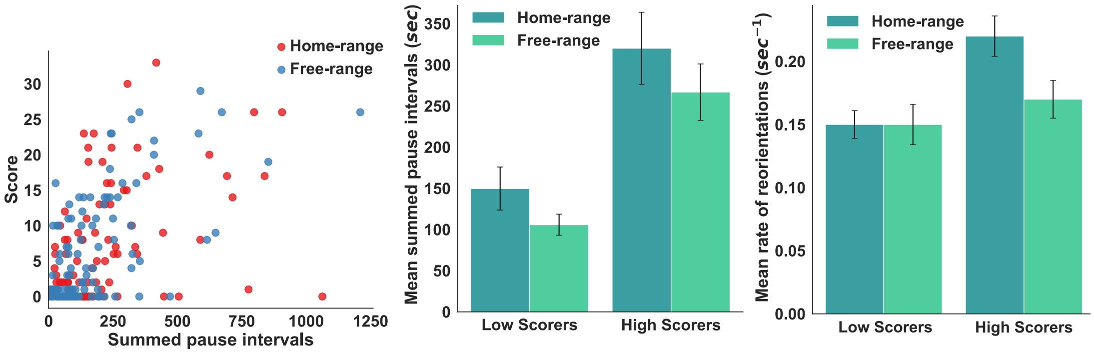


Figure 2.7: **Left:** Summed pause intervals plotted against score and separated by home-range versus free-range foraging. **Center:** Means of summed pause intervals, and **Right:** mean rates of reorientations. Error bars show standard error of the means.

2.5 Discussion

In recent years, there has been a tension between physics-based theories and more cognitive theories of foraging (Pyke, 2019). On the one hand, theories like Lévy walks seem plausible for relatively simpler organisms that search for resources relatively uninformed, with little or no memory or directionality, akin to the random walks of particles. These theories mostly focus on optimal movement and assume perfect perceptual capabilities that allow automatic resource detection. On the other hand, cognitive theories that invoke memory, learning, and decision-making seem more appropriate for humans and other complex organisms (Namboodiri et al., 2016). Such theories rooted in the optimal foraging framework emphasize trade-offs involving time and energy constraints but devalue the role of spatial search in foraging under constraints on information and memory (Zollner and Lima, 1999).

Our results help resolve this tension in the context of a virtual foraging game with realistic human foraging conditions. Foraging behavior looked like an undirected Lévy walk at the level of individual movement segments, but like a directed series of movements and pauses at the level of whole trajectories. Movement segments were unaffected by task constraints and generally more efficient as their power-law exponents approached $\mu = 2$ and pause intervals approached $\mu = 1$. However, movements were clearly not generated by a purely random process when viewed as whole trajectories. Their dispersal respected constraints of the environment and task conditions, and diffusion exponents deviated purposefully from a random walk. To illustrate, the hilly terrain in our virtual Himalayas afforded constraints and opportunities for foraging. As can be seen in Fig 2.2, players tended to move along ridges rather than go down to lower elevations, especially in the home-range condition. These trajectories respected constraints of movement costs as well as opportunities for unobstructed visual search.

Lévy walks are generally indicative of superdiffusive search, but we found Lévy distributions in the movement segments of subdiffusive trajectories with the home-range constraint, as well as superdiffusive trajectories without it. Alternatively, players could have altered the diffusivity of search by changing the distributions of movement segments and deviating from a Lévy distribution to a Gaussian distribution with short or long step lengths. However, this method runs the risk of losing scale-invariant search properties of Lévy walks that are beneficial for sampling a space at a large range of scales, especially in uncertain and heterogeneous environments (Bartumeus et al., 2008; Humphries and Sims, 2014). Our results indicate that players controlled movement directions, but not magnitudes, in a way that adapted Lévy-distributed movements to the relevant range of search scales (Bartumeus et al., 2003; Seuront and Stanley, 2014) given task constraints. The use of directionality also created movement trajectories that varied in their degree of resampling prior locations, unlike a random Lévy walk. Instead, movements were directed to efficiently over-sample the home-base location at the level of trajectories and thereby enact central-place foraging. We did not test how movement might adapt to variations in the distributions of resource locations, but previous studies have found changes in movement segment distributions with respect to patchiness (Bartumeus et al., 2003; Nurzaman et al., 2010). We only used known temples as resource locations for purposes of ecological validity. However, it would be interesting to examine the effects of different resource distributions and energy landscapes on movement segments versus movement directions in a future study.

We found that pauses for perception and planning were also Lévy-distributed regardless of task conditions (Wearmouth et al., 2014), and estimated parameters indicated that efficient foraging benefited from concentrated search effort, as supported by positive correlations between scores and time spent between movements. One role of mental processing was demonstrated in the shift to more visual search in place of less exploration in the home-range condition due to the energetic costs of return trips. Although pauses did not cost energy in the game, they did incur time, effort, and opportunity costs, e.g., spending the time earning money in another task on the MTurk platform (Mason and Suri, 2012; Ross et al., 2010). In future research, it would be informative to test different time costs and their effects on pauses.

The interleaving of movements with pauses for perception and planning is analogous to inter-patch versus intra-patch foraging, respectively (Kamil et al., 1987; Pacheco-Cobos et al., 2019) – movements take foragers to each new patch i.e. vantage point, and visual search exploits the patch until the probability of finding a resource is low enough to plan and execute the next movement. There is a trade-off between the time and energy needed to move along with the opportunity to find new resources, versus the time needed for visual search and planning to fully cover the area. We found that, in the face of more considerable movement costs, home-range players increased the time they spent on exploiting a 'patch'. In general, more efficient foraging balanced these trade-offs to create movement trajectories that were judiciously extended or contracted by way of concentrated bouts of visual scanning, orienting, and planning. Less efficient foraging used relatively shorter pauses and longer movement segments arranged in more random configurations, as evidenced by diffusion exponents closer to a random walk. Our home-range constraint was perceptual and hence not energetic up to a certain distance, but more energetic constraints might elucidate the role of memory and decision-making processes that assess probabilistic costs and benefits of farther excursions while saving energy to return home (Hamilton et al., 2016; Sakiyama and Gunji, 2016).

Our results advocate for integrating physics-based foraging theories with more cognitive approaches to explain how cognition builds on more basic search processes to guide foraging behaviors in humans and other complex organisms. For instance, one approach might posit that Lévy-distributed movement segments serve as building blocks for more cognitively-motivated activities to assemble into movement trajectories. Activities like resource detection, planning, visual scanning would unfold incrementally in bursts of concentrated processing between movements. Previous theories have explained pause intervals in terms of simple models assuming the probability of local target detection increases with longer waiting times (Bénichou et al., 2005). By contrast, our results call for explanations that involve mental processing (de Froment et al., 2014) and optimal foraging predictions (Kamil et al., 1987; Nathan et al., 2008). For instance, concentrated bursts of perception and planning might aid attentional focus (Hills, 2006) similar to area-restricted search. More generally, there is a need to explain how task demands and constraints affect decision processes that span spatial and temporal scales in which local choices over short timescales integrate and interact with broader, longer-range orienting and planning (Brantingham et al., 2006; Farnsworth and Beecham, 1999; Purcell and Kiani, 2016). Models of efficient foraging in natural environments should account for the trade-offs between extrinsic constraints (e.g., energy landscapes, resource distributions, landscape heterogeneity) and cognitive constraints (e.g., limited memory and attention, task switching costs, information uncertainty).

In closing, it has been hypothesized that human intelligence partly evolved from adaptations selected for efficient foraging behavior (Rosati, 2017; Wilke and Barrett, 2009). For example, selective attention may have resulted from the tendency of food and other foraging resources to be clustered in time and space, thereby requiring focus on those clusters and not other potentially distracting features in the environment (Hills, 2006). Likewise, perception and planning decisions may have been shaped by adapting Lévy walks in purposeful ways that adjust to varying conditions and constraints. Such an adaptation may have been co-opted for processes of memory search (Kerster et al., 2016a) and visual search (Rhodes et al., 2014). Understanding the behavioral bases of foraging at different scales (Levin, 1992) may serve as a foundation for studying trade-offs between physical and cognitive costs involved in many aspects of learning and decision-making (Mobbs et al., 2018; Schulz et al., 2018), with implications for broader problems of optimal search and foraging (Hart et al., 2018; Seuront and Stanley, 2014; Shlesinger, 2006).

2.6 Methods

2.6.1 Game environment

The foraging game was implemented in Unity 3D and primarily scripted in C#. The game was modeled on a 5x5 kilometer area in the Himalayas (Top-Left - 32.6548, 76.056530, Bottom-Right - 32.54895, 76.194889). The relief of the terrain was downloaded from Google Earth and rendered in the Unity environment using Infinity Code. Forty-nine temples were identified in the chosen area based on location data from Google Maps. The coordinates of the temples were marked in the Unity landscape, and a model temple was placed at each location. The movement was only forward and backward with turns to change direction, and movement speed was set to be 6m/s. This fast but realistic speed helped foragers cover a greater area and find more temples in a shorter time that is ideal for MTurk studies. A visible energy bar was depleted as a function of the slope approximated from prior studies on movement associated energy expenditure in humans (Minetti et al., 2002). Specifically, a constant minimum was set per meter for flat and downhill surfaces, and the cost increased by 35% for each angular degree of increase in grade. This approximation is a simplification of more realistic functions that consider higher-order effects of downhill slopes on energy expenditure. We also simplified the game by excluding a resting metabolic cost during pauses and turns, and excluding an energetic reward for finding temples. These simplifications made it easy to measure and compare foraging efficiencies while also controlling the length of game play.

Players used six keys to control movement and perspective (‘w,’ ‘a,’ ‘s,’ ‘d,’ ‘up arrow,’ ‘down arrow’), the latter two tilting their line of sight up and down to adjust for sloping terrain. Mouse movements were used for clicking on temples in view when found, and auditory feedback was available with steps to indicate movement, and clicks to indicate successful temple identification. Players were recruited on Amazon Mechanical Turk and the study was approved by the University of California Merced Institutional Review Board. All experiments and analyses were performed in accordance with the guidelines of the review board. Informed consent was obtained and players were given a guided practice trial to acclimate to the game, and its rules and controls. They were instructed to find as many temples as possible before depleting their energy, with the number of temples displayed in the corner of the screen. In the home-range condition, where players clicked on the home-base to report temples, the number of temples found and reported back to base were both displayed. Player scores were based only on the number of temples reported, and to calibrate, players were told that 49 temples existed in the game. Each player was paid a base amount of 50 cents for completing the game, and an additional bonus of 20 cents was awarded for every temple successfully recorded in free-range condition. However, for the home-range condition, the bonus was awarded for every temple reported back to the home-base. Game can be accessed at Home-range and Free-range.

2.6.2 Trajectory Analysis

We computed MSD as a function of energy expended to characterize the type of diffusion:

$$MSD = \frac{1}{n}\sum_{j=1}^{n} < [r(e+\Delta e) - r(e)]^2 >_j \tag{2.1}$$

where *r(e)* is the position vector of the player at energy e, Δ e is the energy expended, n is the total number of players.

2.6.3 Segment Distribution Analysis and Model Selection

The game play for each participant was divided into segments of continuous movement (i.e. the forward or backward key was held down) interspersed with time intervals of no movement, i.e. pause intervals. The length of each movement segment l was the total amount of time spent moving during the segment, which was equivalent to the amount of ground covered because velocity was constant. We discarded segments where l was less than one second.

Distributions of individual movement segments or pause intervals were plotted and analyzed directly, rather than binned into frequency histograms (Clauset et al., 2009). We calculated complementary cumulative distribution functions (i.e. CCDF or 1-CDF) for a given distribution function X, evaluated at every observed segment length, l, where CCDF(l) = $P(X \geq l)$ or the probability of observing segments in a given distribution $\geq l$. CCDFs were plotted simply by rank ordering individual segments along the x-axis, with CCDF(l) on the y-axis. We calculated and plotted individual CCDF for each participant instead of combining them into a single distribution.

We used Maximum Likelihood Estimation (MLE) to fit each distribution to the probability density functions of the most commonly used models in behavioral and foraging studies: Truncated power-Law, Pareto, lognormal, truncated Pareto with an exponential cutoff, exponential, and bi-exponential distributions. MLE finds the

PDF parameters that maximize a monotonic log-likelihood function $\mathcal{L}(\mu)$ such that $\mathcal{L}(\mu_{max}|x) > \mathcal{L}(\mu_{other}|x)$ where x is the data and μ is the fitted parameter.

We estimated the goodness-of-fit between data and model by calculating the log-likelihood values for estimated model parameters, $L = \sum_{i=1}^{n} \mathcal{L}(\mu_{max}|x_i)$, i.e. summation of the likelihood function $\mathcal{L}$ over all n data points in the distribution. We then selected the best model using the Akaike Information Criteria (AIC) which prefers the model with fewest parameters and maximum L. We used the small-sample correction for the AIC when needed. We also calculated Kolmogorov-Smirnov (KS) D statistic between CCDFs of empirical data and model estimates to further check the goodness-of-fit. The KS statistic measures the maximum distance between two distributions, KS results were in agreement with AIC results.

Truncated power-law, bi-exponential and Pareto were the best fitting probability density functions (parameters were estimated numerically):

Truncated power-law:

$$p(x) = \frac{\mu(x_{max}^{\mu} - x_{min}^{\mu})}{x_i^{\mu+1}} \tag{2.2}$$

where parameters estimated numerically were μ and x_{max}.
Power-law:

$$p(x) = \frac{\mu(x_{min}^{\mu})}{x_i^{\mu+1}} \tag{2.3}$$

where μ was estimated numerically.
Bi-exponential:

$$p(x) = Aexp(-\lambda_1 x_i) + (1 - A)exp(-\lambda_2 x_i) \tag{2.4}$$

where A and $1 - A$ are the relative weights of the two modes, and λ_1 and λ_2 are the exponential decay rates.

The bi-exponential model provided good fits to the data, but it was not favored by AIC because of its additional parameter. AIC results showed that a large majority of distributions were best fit by the truncated power-law model. Therefore, as shown in Fig2.4, we plotted CCDFs of each individual distribution and its best-fitted truncated power-law function.

Chapter 3

Individual exploration and selective social learning: balancing exploration-exploitation trade-offs in collective foraging

3.1 Preface

In the previous chapter, we showed that an individual forager can efficiently search for sparse targets by balancing explorative and exploitative search modes (through $\mu \approx 2$), and further by adapting this balance according to their extrinsic and intrinsic constraints. In this chapter, we scale up to the level of a group composed of multiple foragers, and use an agent-based model to study how the optimal individual-level search strategy changes when part of a group under different extrinsic conditions, such as resource environment and group-size. In addition, we also look at the effect of individual-level strategies on the group-level search efficiency.

3.2 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 territory (Bartumeus et al., 2014; Kembro et al., 2019; ?). 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 forgers 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 (Afshar and Giraldeau, 2014; Boyd and Richerson, 1985; Grueter and Leadbeater, 2014; Kendal et al., 2009; Rieucau and Giraldeau, 2011; Rogers, 1988). 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 a "problem space" for solutions to complex challenges.

In this chapter, 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 (Kendal et al., 2005; Laland, 2004; Muthukrishna et al., 2016), 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 (Clark and Mangel, 1986; Ding et al., 2020). 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; Rendell et al., 2010). 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 (Barkoczi and Galesic, 2016; Bond, 2005; Toyokawa et al., 2019). 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.

Individual search strategies help organisms move efficiently and find relevant resources, but in non-spatial domains, they can represent decision-making processes underlying various tasks such as problem-solving (Hills et al., 2012). Collective foraging allows foragers to share findings from individual search and socially learn from conspecifics (Giraldeau and Caraco, 2018). It also represents socially-interacting systems that can act as distributed cognitive systems to improve search (Goldstone and Gureckis, 2009). However, the interplay of individual search strategies and collective search remains largely unexamined. 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. However, explorative search can cause foragers to exit a patch without fully exploiting it.

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.

3.3 The Model

3.3.1 Model Overview

We modeled the explore/exploit trade-off in individual search using a Lévy walk model. 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., 1999) and has been widely documented in various search processes across domains (Namboodiri et al., 2016; **?**; **?**). 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. Prior empirical and computational studies have found that $\mu \approx 2$ (Garg and Kello, 2021; Viswanathan et al., 1999) 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/reliability of social information or the expected pay-off from social learning decreased as distance to the cue increased because resources were likely to decrease or disappear entirely in the time needed to travel long distances (Beauchamp, 2008; Seppänen et al., 2007). Therefore, we operationalized *selectivity* in social learning or responsiveness to social cues through a parameter α, which modulated the probability of scrounging as a function of distance to social cues (Harpaz and Schneidman, 2020). Selectivity in the model represented social learning in naturalistic settings where organisms conditionally use social cues based on their reliance and costs of social learning (Galef and Laland, 2005). The parameter 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 (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 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. We designed this model with the goal to simulate coarse-grained collective foraging for exploring the fundamental dependencies between social learning and independent, individual search, and how they influence group performance. We did not simulate a specific system or organism, instead we provide a basic framework that resembles many natural systems and which can be built upon to model a specific system and make explicit predictions about it (Smaldino, 2017).

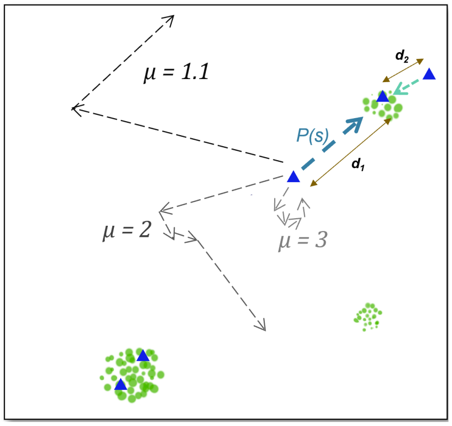


Figure 3.1: A schematic of the model. Agents (blue triangles) decide between individual exploration and using social information based on $P(s) = \exp(-\alpha d)$ to copy a resource location (green circles) found by another agent. For $\alpha > 0$, $P(s)$ will be higher for d_2 than d_1. The level of individual exploration is dependent on μ, where $\mu \to 1.1$ results in high levels of exploration (See Fig.A.2 for actual trajectories and Fig.A.3 for the relationship between α and distance).

3.3.2 Model Details

The search space was a two-dimensional $L \times L$ grid, and simulations were run with periodic boundaries, and continuous space. 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.A.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

$$P(d) = C{d_r}^{-\beta} \tag{3.1}$$

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

$$C = \frac{1-\beta}{(L)^{1-\beta} - (d_{min})^{1-\beta}} \tag{3.2}$$

β determined 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. 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 were determined by either individual search strategy or social learning (see below). Similar to a model by Bhattacharya et al. (Bhattacharya and Vicsek, 2014), 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. In other words, we assume that the agents had a perceptual range limited to radius, r ($r = 10^{-3}$) for resources that did not emit signals other than direct visual cues, whereas social cues are assumed to be similar to acoustic signals or chemical gradients that can be perceived at long distances. This assumption models realistic foraging scenarios where social cues can substantially increase the perceptual range of a forager and improve prey detection or patch sensing over larger spatial scales (Ward and Webster, 2016). For example, birds can detect the pecking behavior of a conspecific from a greater distance than they can detect an individual seed, or scavenging birds can detect a conspecific circling a carcass from many kilometers away.

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

$$P_S = \exp(-\alpha d_{ij}), \tag{3.3}$$

where d_{ij} was the distance between agents A_i and A_j, and α was the social selectivity parameter 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. $\alpha \to 0$ corresponded with minimally-selective/indiscriminate exploitation of social cues (Fig.A.3) where agents were more likely to engage in social learning irrespective of distance costs. In other words, the agents exploited social information more frequently. Intermediate values ($\alpha \approx 10^{-2}$) corresponded with selective social learning, where exploitation of social information was less likely for more distant signals.

And $\alpha \to 1$ corresponded with extreme social selectivity that resulted in no social learning or social information use 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. While pursuing a social cue, an agent kept their target location fixed that did not change even if the agent that emitted the cue moved to another location.

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,

$$P(d) = Cd^{-\mu} \tag{3.4}$$

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, and μ is the power-law exponent, $1 < \mu \leq 3$. Similar to

Eq. 3.5 C, is a normalization constant such that

$$C = \frac{1-\mu}{(L)^{1-\mu} - (d_{min})^{1-\mu}} \tag{3.5}$$

The Lévy exponent μ modulated the search strategy as a continuum between shorter, more exploitative movements and longer, more explorative movements. 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 reduces their value. Model details are also outlined in a flowchart in Appendix A (Fig.A.4).

Our model did not have any explicit fitness costs; however, there were various costs associated with optimal searching and foraging, such as opportunity costs and competition. For instance, the resources were limited and did not regenerate, and as more agents reached a patch, the resources depleted, and the agents who followed a cue to walk to that patch faced substantial opportunity costs. 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. Here we report parameter values that affected explore/exploit trade-offs in individual search as well as social learning.

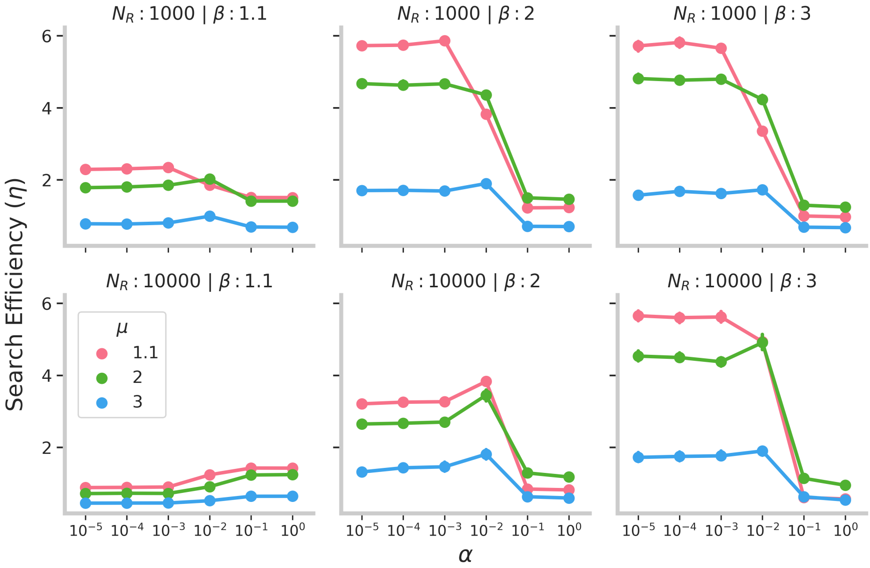


Figure 3.2: Group search efficiency η for $N_A = 10$ as a function of social selectivity parameter α, Lévy exponent μ, resource density N_R, and resource clustering β. Error bars indicate 95% confidence intervals.

In the Appendix, we report results on the effects of resource environments, individual search strategies, and group sizes for groups composed of pure producers ($\alpha \to 0$) and scroungers ($\alpha \to 1$) (Figs. A.11a, A.11b). We also report the population-level variability in observed Lévy exponents and search efficiencies (Figs. A.8). In addition, we illustrate how resources depleted over time in our simulations, and changes in average Lévy exponents and search efficiencies over time for a few parameters (Figs. A.9, A.10.

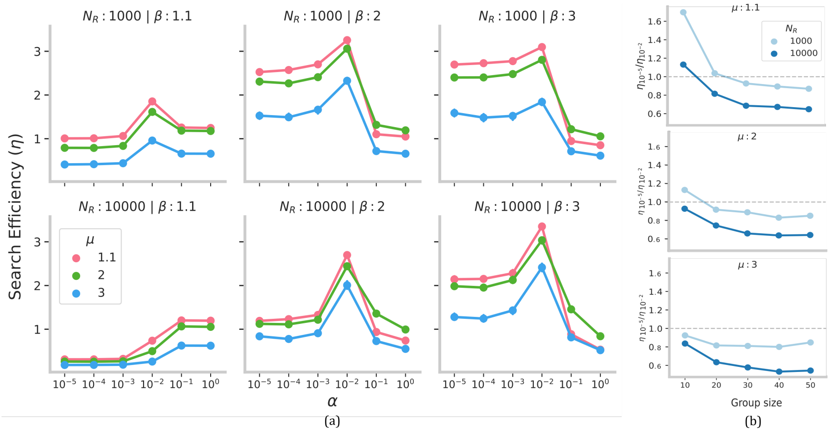
3.4 Results

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

We tested whether agents should trade-off individual search for social learning under two different conditions of rich and scarce resources, and three levels of clustering. We found that when resources were scarce ($N_R = 1000$; top row of Figs. 3.2 and 3.3)), irrespective of clustering, 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 Figs. 3.2 and 3.3). Scarce resources were not only challenging to find through random independent search, but the opportunities to use social information were also far and few. However, when environments were rich ($N_R = 10000$; bottom row of Figs. 3.2 and 3.3)), social learning was only beneficial if resources at least were moderately clustered (in $\beta \geq 2$). By contrast, individual search rather than social learning ($\alpha \geq 10^{-2}$) was beneficial when resources were abundantly dispersed across the landscape ($\beta = 1.1$) because the likelihood of encountering resources increased by random sampling and decreased after following social cues. On the other hand, groups benefited considerably from social learning when social information was more reliable in highly clustered environments with dense clusters ($N_R = 10000$; $\beta = 3$). In clustered environments, the probability of finding more resources within the vicinity of a social cue was high (Fig.A.1)), and pursuing social cues helped agents to find resources while decreasing the costs of more error-prone individual search. Furthermore, it enabled a form of collective 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.

3.4.2 Social learning affected the optimal Lévy exponent and its benefits were maximized with explorative individual search

When α values were high (rightmost two points of each plot in Figs. 3.2 and 3.3), agents did not respond to social cues (or were highly selective), and Lévy walks drove individual search. Our results show that Lévy walks with $\mu = 2$ were most efficient in the absence of social learning. This effect 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 resembling area-restricted



(a)

(b)

Figure 3.3: ***(a)*** Group search efficiency η ($N_A = 50$) as a function of social selectivity parameter (α) for different Lévy exponents (μ), resource density (N_R) and resource distribution (β). Error bars indicate 95% confidence intervals. ***(b)*** Effect of group size and individual search strategy on the advantage of minimally-selective social learning strategy ($\alpha = 10^{-5}$) 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.

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 $\mu = 1.1$. 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 $\mu \to 1.1$ (see section 3.4 for more details). 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 and larger sizes benefited more from selective social learning relative to minimally-selective social learning (Fig.A.5). We explain this result in the next section.

3.4.3 Selective social learning was 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 $\alpha \to 10^{-5}$ 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 them 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.

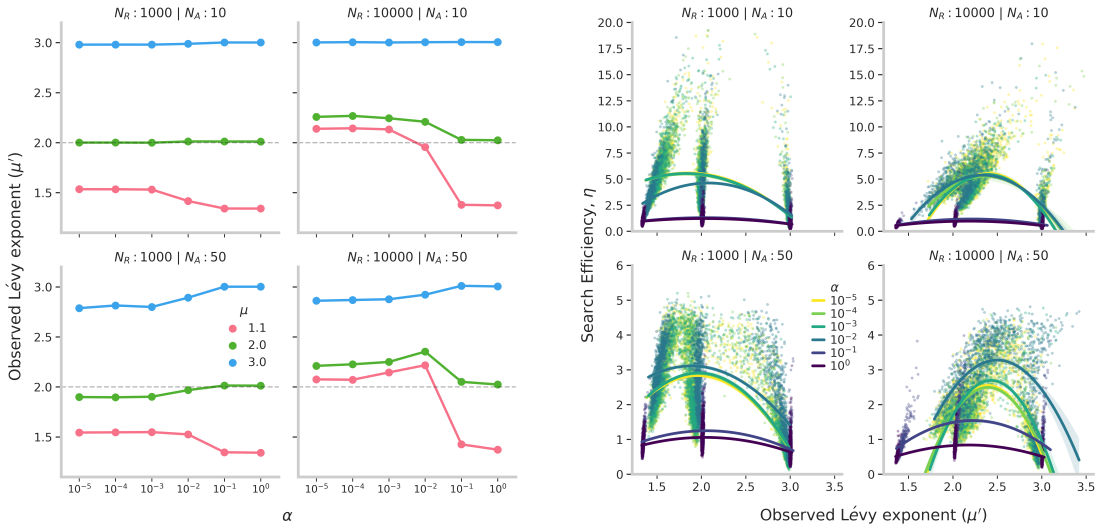
To illustrate, imagine that an agent happens upon a cluster of resources. It sends a resource signal, and another agent heads towards the cluster. They both find more resources in the cluster, and that increases the time they spend there. In turn, chances are increased of other agents responding to their 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. The snowballing effect in our model closely resembles the positive feedback loops and social amplification phenomenon observed in different collective systems such as bees and ants (Detrain and Deneubourg, 2006).

When agents' individual search strategy was closer to a Brownian walk ($\mu \approx 3$) with frequent turns and short movements, minimal selectivity (or excessive social learning) led to more substantial grouping between the foragers and restricted them to small areas of the environment for longer durations (Fig.A.12b). Thus, a more selective social learning strategy decreased the grouping between the agents and increased group performance (Fig.A.5). 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 group size increased (Fig.3.3), the benefits of minimally-selective social learning relative to selective social learning further decreased. A larger number of agents exaggerated the chances of snowballing that further drove up the competition over resources, decreased the value of social cues, and reduced the individual exploration for other resources. For instance, over-exploitation of social information ($\alpha = 10^{-5}$) in larger groups caused agents to aggregate together in bigger sub-groups (Fig.A.12a), and for longer durations (Fig.A.12b), which decreased the group-performance (see Fig.A.9, A.10 for temporal dynamics of this pattern).

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 Fig.A.12d (right) and A.12c). 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.3.3). 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



(a) (b)

Figure 3.4: ***(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.

beneficial for them to be selective and reduce exploitation of social information ($\alpha = 10^{-2}$) to maintain exploration at the group-level. Conversely, decreasing selectivity ($\alpha = 10^{-5}$) 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 information was necessary to prevent groups from snowballing and effectively maintain a balance between group-level exploration and exploitation.

3.4.4 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 3.4a (top), see Supplementary Methods in Appendix A for details on this analysis). Here we report the average values of μ' across agents within a group. In the Appendix, we also report examples of population-level values of μ' in a group, the correlation between individual agents' μ' and η (Fig. A.8), and how average μ' changes over time (Figs. A.9, A.10). These additional analyses show that the patterns reported below are consistent across different simulations. To illustrate the distribution of movements, we also provide the empirical probability distribution of path segments and their corresponding fits for a few parameter combinations (Figs. A.7a, A.7b).

We found that with the use of social cues, exploratory walks ($\mu = 1.1$) were truncated, resulting in trajectories with μ' closer towards the theoretical optimum of 2. Thus, it was beneficial for social learners to engage in explorative, independent search and replace exploitative movements driven by random Lévy walks with exploitative search driven by more reliable social cues. 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. 3.4a (top)). However, when the 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; Salvador et al., 2014).

These effects were also reflected in larger group sizes (Fig. 3.4a (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 area-restricted or 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. These patterns were also reflected in the changes in μ' over time (see Figs. A.9, A.10). Moreover, we found that when the individual search strategy was exploitative and comprised of short steps ($\mu = 3$), social learning gave rise to trajectories $\mu' \to 2$ 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 $\mu \approx 2$.

3.5 Discussion

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 by dampening exploration for new solutions. Results from the current study 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 addition, we show that socially-guided exploitation of resources can be substantially more beneficial than trial-and-error based Lévy walks. In the following paragraphs, we first discuss the interplay between individual search and social learning, and its relevance to the Lévy walk literature. We then discuss the effect of selective social learning in modulating explore/exploit trade-offs and its broader implications on collective foraging and problem-solving.

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. 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 resources were scarce and clustered (Egert-Berg et al., 2018; Rafacz and Templeton, 2003; Smolla et al., 2015). Scarce and clustered resources made it difficult for agents to independently/asocially find them while increasing the likelihood of finding more resources after following social cues. This result also agrees with previous findings on social insects that show the positive effect of social recruitment in spatially clumped resource environments (Donaldson-Matasci and Dornhaus, 2012; Lemanski et al., 2021). However, our results show that the benefits of social learning depended on individual search strategy and could be maximized by explorative search. We found support for previous studies (Garg and Kello, 2021; Viswanathan et al., 1999) which have shown that independent search is optimal when individuals balance the explore/exploit trade-off with the Lévy exponent of 2 ($\mu \approx 2$) in the absence of information about the environment. We found that 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 and to balance it with high levels of random exploration. 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. In this way, groups can balance finding new resources quickly and accurately exploiting the resources found.

Furthermore, 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 the 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 (Ferreira et al., 2021), suggests an alternative heuristic that can be used to optimize collective search, and contributes to understanding how information can guide agents to increase their search efficiency (Salvador et al., 2014). It is possible that in natural environments with cognitive foragers, informed foraging decisions backed by memory, perception, and learning (Benhamou, 2007; Garg and Kello, 2021; Kerster et al., 2016b; Miramontes et al., 2012; Ramos-Fernández et al., 2004) 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 search. To shed light on more realistic aspects of social foraging, it would 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 (Dall et al., 2005; Grüter et al., 2008).

Our model also tested the optimal degree of selectivity on the benefits of social learning under varying conditions. The social selectivity parameter, α simulated a minimal heuristic that modulated the use of social information based on its costs (distance and opportunity). 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)), leading to large and prolonged subgroups of agents, and suppress exploration for new resources. We found that selective social learning ($\alpha \approx 10^{-2}$) "filtered" 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.

Excessive convergence between individuals within a group and the formation of optimal sub-groups can be modulated through other mechanisms, as well. 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 avoid excessive overlap. Adaptive sub-grouping 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). Previous studies have shown that separation and convergence between individuals can also be modulated by adjusting local interaction rules (such as alignment with others, range of interaction or communication) depending upon the context (Beecham and Farnsworth, 1999; Harpaz and Schneidman, 2020; Hoare et al., 2004; Martínez-García et al., 2013). Similarly, the selectivity parameter in our model can also represent different effective perceptual ranges where lower and higher values of α simulate large and small perceptual or detection range, respectively. The model can be extended with a hard-limit on how far an agent can detect other agents in its environment, and test how that changes optimal strategies and sub-grouping. Our results predict that groups can decrease competition, increase discovery of new resources and their foraging returns by balancing overall inter-agent separation (or exploration) and convergence (or exploitation).

Although we simulated collective foraging, our 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). Our results predict that high explorative/innovative tendencies can improve a group's problem-solving capabilities in a complex problem-space where multiple solutions need to be discovered by mitigating over-imitation, escaping being stuck in local optima and increasing informational diversity (Hong and Page, 2004; Sloman et al., 2021; Toyokawa et al., 2019). However, we also predict that 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. By contrast, when the problem spaces are 'simple', 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 support the importance of optimal connectivity and information-flow in groups for problem-solving and collective behavior (Barkoczi and Galesic, 2016; Bernstein et al., 2018; Derex and Boyd, 2016a; Garg et al., 2021; Goldstone et al., 2013; Gomez and Lazer, 2019). Like a densely connected group with unrestricted information-sharing, excessive levels of overall social learning in a group can decrease exploration and cause individuals to converge on sub-optimal solutions while preventing them from exploring other profitable solutions (Bikhchandani et al., 1992; Giraldeau et al., 2002; List et al., 2009). However, we predict that selective social learning can mimic partially-connected groups and balance the global search for new solutions (or innovations) and local search near the solutions previously found.

Our model focused on group-level performance, determining the individual strategies that maximize group efficiency. However, there is no guarantee that strategies that optimize collective performance will be evolutionarily stable (Clark and Mangel, 1986). For example, Rogers (1988) analyzed a model in which naive social learners could invade a population of individual learners, initially increasing mean fitness. However, the social learners continued to increase in frequency until the mean fitness of the population decreased to its initial level, equivalent with a population of entirely individual learners. The analyses presented here are unable to assess the conditions under which a population will evolve to optimally extract resources from the environment. We did conduct additional analyses, presented in the Appendix, with heterogeneous groups in which individual agents differed in their propensity to socially learn from others—i.e., the population contained a mix of producers and scroungers. We found that different relative frequencies of producers and scroungers led to optimal foraging outcomes at the population level under different assumptions of population size and resource distribution (Fig. A.11a, A.11b). Nevertheless, further extensions of the model with evolutionary dynamics would be required to assess the evolutionary plausibility of these optimal group outcomes.It would also be interesting to analyze if agents within a group vary from each other in terms of search strategies and efficiencies, and how such inter-individual variability affects group-level performance.

In conclusion, our results are applicable to various distributed, collective and socio-cultural systems, and general search heuristics. Trade-offs between the exploitation of previously found resources or solutions and exploration for new ones is fundamental to adaptive behavior in individuals and groups (Fang et al., 2010; Hills et al., 2015; March, 1991). Our coarse-grained model explored this fundamental trade-off at both individual and social level, and how they influence group performance. Although different systems may modulate these trade-offs through different mechanisms, our results predict that their modulation should be important across many systems.

For example, social insect colonies can balance these trade-offs and increase efficiency through division of labor (or task allocation) where individuals can specialize in searching for new resources or exploiting the ones found (Lemanski et al., 2021). Future models can test for the emergence of different mechanisms under varying physical and social environments, and further shed light on the evolution of group-living, social learning, and cultural evolution.

Chapter 4

Evolutionary dynamics of search strategies in collective foraging

4.1 Introduction

As shown in the previous chapter, collective foraging and social learning can be advantageous in patchy resource environments for groups composed of individuals who show high levels of independent exploration while using social information to minimize search costs. However, strategies that increase performance at the population-level may not always be evolutionarily stable and can get exploited by other lesser beneficial strategies in groups. In this chapter, we ask how individual-level search strategies evolve under different levels of social learning, resource environment, and, group size, and whether the evolutionary stable strategies promote similar levels of group-level search performance as in the previous chapter. We further show that both individuals and groups can improve their foraging efficiencies by employing simple and widely-observed heuristics like area-restricted search.

For a solitary forager, it is essential to adopt search strategies that enable exploration of an environment to sample new information along with sufficient exploitation of the resources found. Multiple theories of optimal foraging have suggested that this trade-off can give rise to movement patterns that modulate the balance between explorative and exploitative modes of search (Charnov, 1976; Viswanathan et al., 1996) based on the properties of the resource environments, such as patch richness, and travel time between patches. For instance, when patches are rich but not easy to find, then search strategies that prolong exploitation of a patch, such as movements closer to a Brownian walk, would be optimal (Kölzsch et al., 2015). Conversely, a faster rate of depletion of resources in a patch should favor strategies that allow early departure from the patch (Charnov, 1976; Krebs et al., 1978). However, when a forager is a part of a group of multiple foragers, and they aggregate together, patches may deplete at an even faster rate and promote strategies with an even faster dispersal to maximize the payoffs. On the other hand, collective foraging can help individuals harvest a patch more effectively, accelerate the rate at which groups find resource patches, decrease search costs. Thus, the optimal search strategies and the balance between explorative and exploitative search in collective foraging would be influenced by the resource environment structure as well as its social environment.

Collective foraging confers several benefits to an individual forager by making available the information gathered by other group members at lesser personal search costs, increase the rate of resource discovery if foragers do not overlap in their search area, and even more effective exploitation of patches (Hein and McKinley, 2012). However, on the other hand, these apparent advantages can increase the competition for resources, cause overcrowding at patches and accelerate resource depletion, and increase the costs of collectively foraging. Moreover, the costs and benefits of collective foraging may not be equally distributed between group members. Individuals with explorative search strategies, who are more likely to discover new resources and contribute to the group's overall performance, might be at a disproportionate disadvantage if they cannot fully exploit the patches they find, especially if their tendency to explore decreases the time they spend in a patch. On the other hand, individuals with exploitative search strategies who rarely discover new resources but thoroughly exploit a patch might benefit the most from information sharing in groups, especially when patches are dense with resources.

Such asymmetrical payoffs between different strategies can result in dynamics similar to producer-scrounger games, where some individuals 'produce' information by independently finding new resources while others 'scrounge' or exploit the patches found by producers without contributing to the discovery of new options (Barnard and Sibly, 1981). These dynamics can often cause the payoffs of one strategy to depend upon the frequency of the competitor strategy, such that the payoffs of a strategy would be low if the number of agents practicing another strategy is high, and result in a mixed evolutionarily stable strategy, where neither does better than the other. Further, an increase in scroungers or social learners can decrease a group's overall performance (Rogers, 1988). Thus, an individual forager would need to adapt its search strategy based on the behavior of its group members to ensure that it maximizes its resource gain while decreasing the many costs associated with collective foraging, such as competition, opportunity cost, and search cost (Rita et al., 1997).

Previous studies have shown that individuals in many animal groups can consistently differ from each other in their search strategies, especially in terms of risk-taking, bold or explorative behavior (Dingemanse et al., 2003; Mehlhorn et al., 2015; Reader, 2015; Réale et al., 2007). Explorative individuals tend to be risk-prone, move long distances, and often lead their groups. On the other hand, shy or exploitative individuals tend to be risk-prone and show high group cohesiveness (Aplin et al., 2014; Ioannou and Dall, 2016; Ward et al., 2004). These characteristics of explorative and exploitative individuals can affect many decisions relevant to foraging. For instance, the speed of exploration could directly affect the rate of resource discovery, overlap in search areas, and even the time spent exploiting a patch (Patrick et al., 2017). It has been shown that individual differences along the explore-exploit continuum can affect the social behavior such as flocking, coordination (Aplin et al., 2014), and have important consequences for collective foraging (Dyer et al., 2009). However, how the individual search strategies are in turn affected by social behavior and by the costs and benefits of collective foraging has been understudied.

In the following study, we study the evolution of different search strategies along the exploration-exploitation continuum under several levels of social learning, group size, and resource density that manipulate the costs and benefits of the search strategies in collective foraging. As shown in the previous chapter, exploratory strategies cover a greater area of space and have a higher chance of encountering new and undepleted patches. However, they also tend to exit patches before exploiting it thoroughly. Thus, when competing for resources, exploitative strategies can take advantage of the patches discovered and left largely unexploited by the explorers. This effect could lead to a mixed evolutionary stable strategy (ESS) where neither explorers nor exploiters can completely invade a population.

We predict that the proportion of explorers and exploiters in evolved groups would depend upon the level of social learning, group size, and resource density. For example, the payoff from exploiting would be higher in environments with rich patches, but it may decrease if the frequency of social learning in the group is high. High levels of social learning could increase the aggregation of agents on a few patches, increasing competition and decreasing the benefits of exploiting while increasing the payoffs from an explorative strategy that helps agents exit an increasingly crowded patch faster. On the other hand, selective social learning may limit the ability of exploiters to use social information, decrease their payoffs, and promote exploration. Moreover, the degree of exploration or exploitation of the evolved strategies may depend on their physical and social environments. For instance, rich patches with higher expected return rates might promote explorer strategies that can balance exploration with exploitation. Further, if explorers can effectively harvest a patch before others join in, it would increase the proportion of explorers in a group. Finally, we predict that groups may not always evolve to maximize their performance and could face diminishing search efficiencies if many exploiters are present in a group.

4.2 Model overview

This study uses an evolutionary model of collective foraging and analyzes how individual search strategies evolve in a group under different conditions that manipulate the extent of competition and facilitation. Using the Lévy-walk model, we simulate a suite of search strategies along the exploration-exploitation continuum. In the model, a power-law parameter, μ, specifies the composition of long and short movements in a search trajectory and can closely simulate the empirically observed features associated with explorative and exploitative strategies. For example, agents with $\mu \to 1$ have a trajectory that is primarily composed of straight-line movements that helps them cover an area quickly and find new patches at a faster rate than less explorative agents, but they also may cause them to exit a patch without sufficiently depleting it.

We further test whether the evolved search strategies promote similar levels of group-level search performance as in the previous chapter. We should expect an increase in group search efficiency with an increase in exploratory individuals, which is the most optimum strategy for groups. However, it is possible that the group efficiency does not increase over time if the payoffs from exploratory strategies are not higher than the exploitative ones. Finally, we modify the model to include a more informed form of search to the strategies, namely area-restricted search that could affect the payoffs from the strategies. Many studies have shown that animals and humans perform an area-restricted search strategy (ARS) that can drive the switch between exploration and exploitation in a more informed manner (Kareiva and Odell, 1987; Pacheco-Cobos et al., 2019). As a simple heuristic, ARS triggers slower and exploitative movements after encountering a resource that intensifies the search in a patch before continuing wide-ranging exploration for new resources. We predict that in collective foraging, ARS could increase the payoffs from exploratory strategies that can now get a greater share of resources after finding new, undepleted patches and also affect group performance.

4.3 Model Details

4.3.1 Evolutionary model

Using the model described in Chapter 4, we tested the evolution of independent search strategies for three values of social selectivity ($\alpha = 10^{-5}, 10^{-2}, 10^{0}$) that represent minimally-selective, selective, and no social learning, respectively. Instead of testing for different resource distributions as in the previous chapter, we focused on the most patchy environment ($\beta = 3$) because it represents an ideal framework to study the effects of both the costs and benefits of collective foraging. To model search strategies, we considered the following six alleles defined by μ: $[1.1, 1.5, 2.0, 2.5, 3.0, 3.5]$, where $\mu \rightarrow 1.1$ represents a highly explorative strategy with fast, linear movements and $\mu \rightarrow 3.5$ results in a highly exploitative strategy composed of short displacements and frequent turns.

Every simulation began with a group composed of agents with uniformly distributed values of μ and contained equal proportions of the six alleles. The evolutionary algorithm selected agents based on their efficiencies to generate a new population after 30% of resources had been consumed. To do so, we normalized the efficiencies of all agents and assigned each with a probability to replicate that was weighted by their normalized efficiency values. For example, consider a group of 5 agents with the following efficiencies at the end of a run: $[0.5, 10, 3, 4]$, which would be then normalized to $[0., 0.61, 0.16, 0.23]$, and their normalized score would weight the probability of each agent to reproduce. In addition, we added a mutation rate of 0.05, such that with a probability 0.05, a randomly picked value of μ was assigned to a randomly chosen agent at the time of selection. Every new group of agents started at random locations with search efficiencies set to 0.

4.3.2 Area-restricted search model

To test the effect of more informed search strategies and of higher payoffs from discovering an undepleted patch, we modified the agent search behavior such that upon finding any resource, agents engaged in an area-restricted search. As a simple heuristic, ARS triggers slower and more tortuous movements after encountering a resource that intensifies the search in a local area before continuing wide-ranging exploration for new resources. In the model presented above, agents could only perceive resources that were present in their current location ($r_v = d_{min}$) and not beyond that. However, many real-world organisms tend to search nearby areas after successfully finding targets. We added a function where agents expanded their radius of vision (r_v) after encountering a target. More specifically, upon finding and depleting a resource patch, agents first searched for resources in the cells neighboring theirs ($r_v = 2d_{min}$) before searching for other successful agents or drawing a step of random-length based on their value of μ. If they found a resource in the neighboring cells, they moved there and consumed the resource.

4.3.3 Evolutionary analysis

The results presented here are from 40 simulations, and each simulation was run for 3000 generations. We measured the evolved values of μ for each parameter combination and for both models (non-ARS and ARS) and the group search efficiencies of the evolved groups. The results below show both the mean evolved μ in populations and their distribution across populations, mean search efficiencies (η), and the changes to μ and η over generations. We would like to note that our model results in stochastic evolutionary dynamics due to more realistic settings such as finite population sizes, stochastic resource environment, stochastic search decisions, spatial interactions, and mutations. The stochasticity prevents the groups from evolving to stable strategies, and to corroborate our findings from the evolutionary model, we performed an invasion analysis with the model to test the likelihood of a strategy invading a population of another strategy based on their relative payoffs. 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 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:

$$i(\mu_{resident}, \mu_{mutant}) = \frac{\eta_{\mu_{mutant}}}{\overline{\eta}_{\mu_{resident}}} \tag{4.1}$$

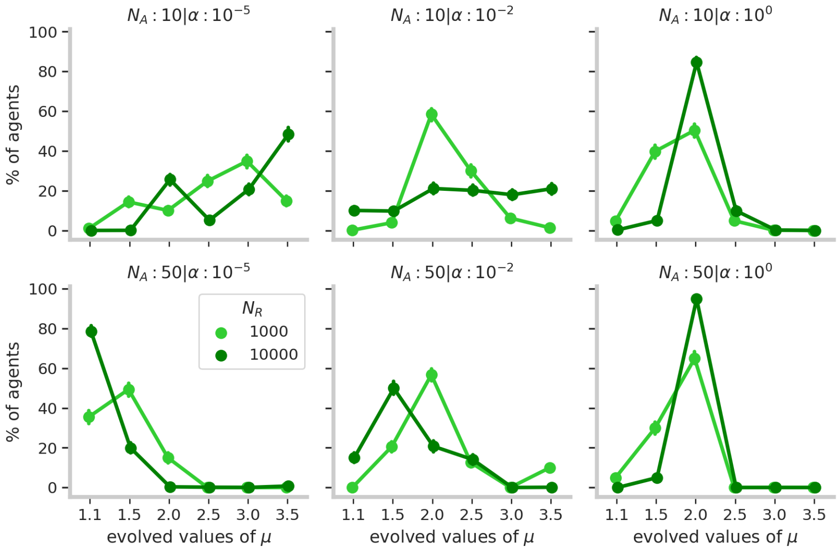


Figure 4.1: Distribution of the evolved values of Lévy exponents (μ) for different levels of resource density (N_R), group size (N_A) and social learning (α). These data represent group compositions over the last 10 generations out of a total of 3000.

4.4 Results

4.4.1 Intermediate levels of social aggregation led to a mixed ESS between explorers and exploiters, but the degree of exploration and exploitation depended upon the environment.

In the previous chapter, we found that groups composed of highly explorative searchers ($\mu = 1.1$) maximize group-level search efficiency. However, a high speed of exploration might not be an optimal strategy at an individual-level. In our model, exploration speed has a positive relationship with the rate of resource discovery and an inverse effect with the time they spent exploiting a patch (or their 'patch-residence' time). While highly explorative searchers will discover resources more efficiently, they will also be more likely to exit the resource patch quickly without fully depleting it, which exploiters can then access.

We found that in small groups where competition for resources is low, exploiters

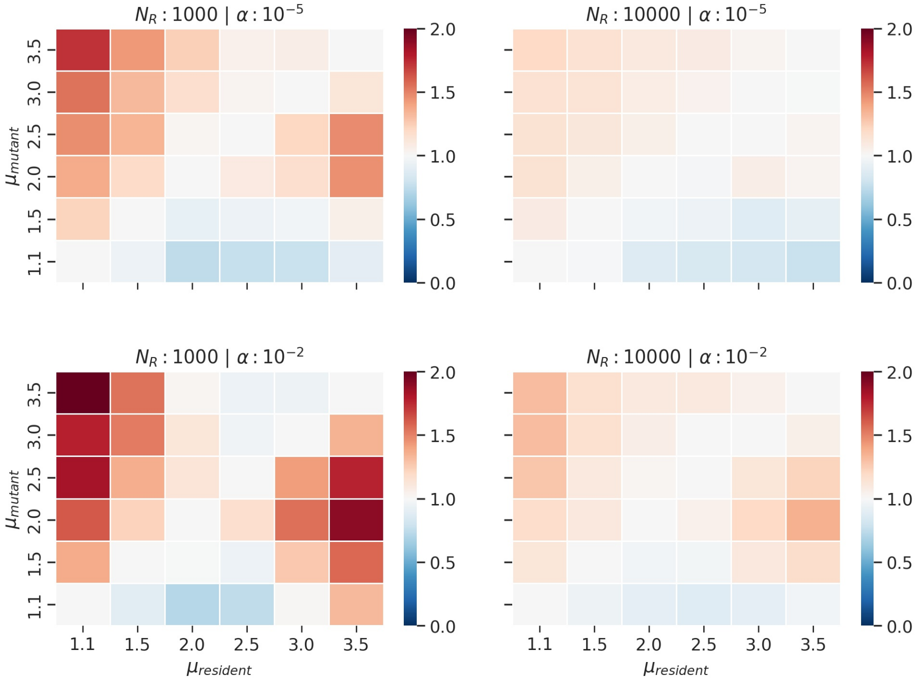
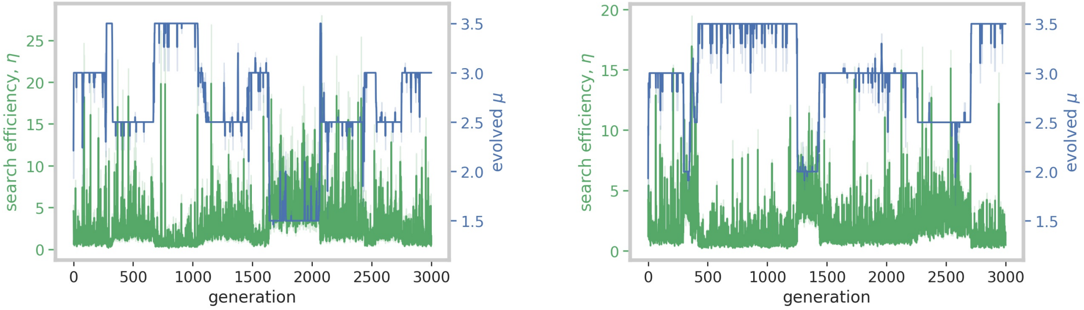


Figure 4.2: Mean estimates of invasion index for groups of size 10, different levels of resource density (N_R) and social learning (α) over 500 simulations. Index values greater than 1 imply that the mutant μ will be over to invade the resident μ.

can increase their foraging returns by reaching undepleted but discovered resource patches and invade populations of fast explorers (Fig. 4.2). However, an increase in the number of exploiters in a population decreases the benefits of collective foraging because of the slower rate of resource discovery, fewer opportunities to scrounge, and higher competition between them. Under such conditions, an explorer may be able to invade a population of exploiters if the amount of resources it consumes before others arrive is comparable with the exploiters' share. However, an increase in explorers can again increase the relative advantage of exploiters due to a higher rate of resource discovery. We can see this pattern in the invasibility analyses where (Fig. 4.2 (top-row)) exploitative mutants can invade explorative populations, but exploitative populations can in turn be invaded by explorers. Our results show that this dynamic can lead to a mixed ESS, where evolved populations are composed of both explorative and exploitative strategies (see Fig. 4.1 for overall composition of the evolved groups and Figs. B.2, B.3 for composition of groups in individual simulations).

While exploratory and exploitative strategies could mutually invade each other under certain conditions, the degree of exploration of the selected strategies can change with resource environments (Figs. 4.1, 4.3). We found that in scarce conditions ($N_R = 1000$), where it was advantageous to exit a patch early and switch to exploring for other options, the evolved strategies were more explorative than in richer conditions ($N_R = 10,000$) that favored spending longer exploitation time in patches. In other words, the evolved groups in the scarce conditions were primarily composed of exploitative agents (with $\mu = 2.5, 3$) and explorative agents (with $\mu = 1.5, 2$). By contrast, in rich patches, the likelihood of fast explorers ($\mu < 2$) invading a population of exploiters decreased, especially slow exploiters ($\mu = 3.5$). As a result, the evolved groups were primarily composed of agents with $\mu = 3.5$ and a smaller proportion of explorers with $\mu = 2$ that could increase their share of the patch before the arrival of other agents.

Strategies with $\mu = 2$ were also less likely to be invaded by other strategies under conditions of very low or no aggregation at patches, for example, with selective or no social learning ($\alpha = 10^{-2}, 10^{0}$). For selective social learning ($\alpha = 10^{-2}$), where agents



(a) $N_R = 1000$

(b) $N_R = 10000$

Figure 4.3: 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 $\alpha = 10^{-5}$.

only responded to social cues that were not very far, the likelihood of agents aggregating at a resource patch decreased and led to very low levels of both competition and aggregation at patches, especially in scarce conditions. Further, responding to social cues in selective social learning depended upon the exploration speeds of agents, where fast explorers quickly diffused away and could miss out on the transient social cues. Exploiters remained confined to certain pockets of the space and were not able to respond to cues in other locations.

Similar to conditions with no social learning ($\alpha = 10^0$), we found that in scarce patches, a search strategy close to $\mu = 2$ that could sufficiently exploit the patch before exiting it, and thus, was not very likely to be invaded by more explorative or exploitative strategies (Fig. 4.2). However, richer patches increased the time agents spend there, increasing the chances for other agents to respond to the social cues. Thus, it increased the payoffs from more explorative and exploitative strategies and $\mu = 2$ became more likely to be invaded. Taken together, these results suggest that when the aggregations at patches are not very low and can facilitate collective exploitation of the patches, both exploratory and exploitative strategies can mutually invade each other and lead to a polymorphic equilibrium. However, excessive aggregation and competition at patches can modify this equilibrium, as we discuss below.

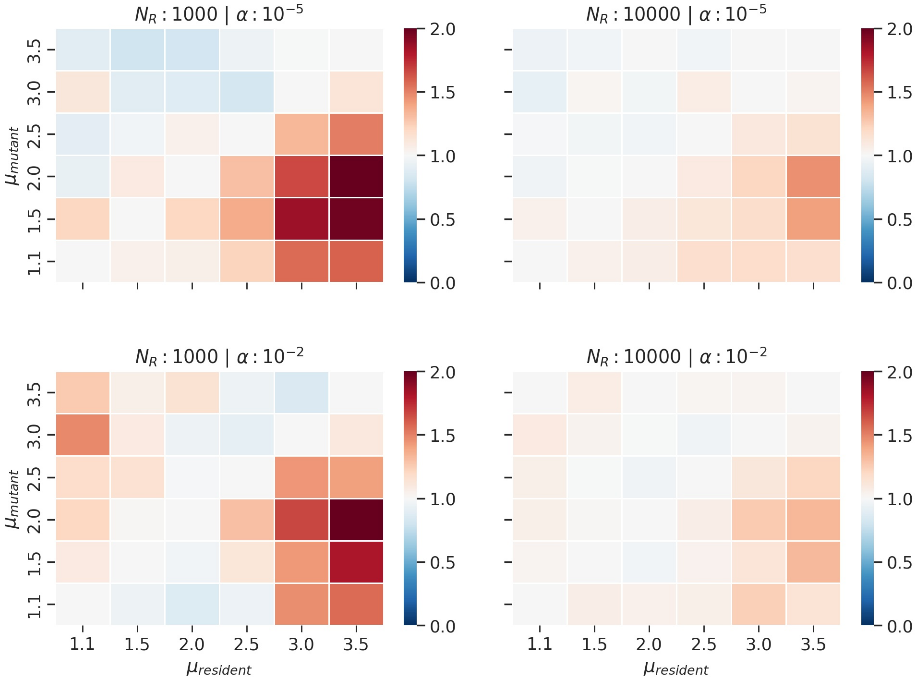


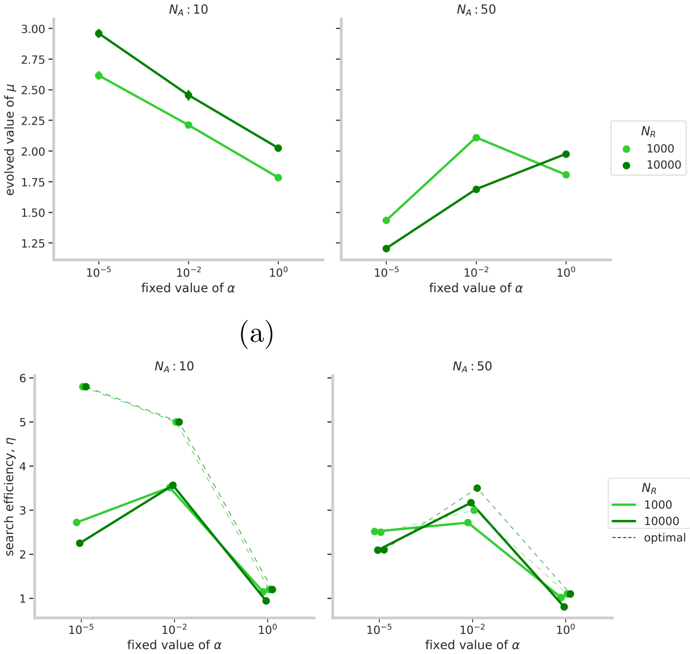
Figure 4.4: Mean estimates of invasion index for groups of size 50, different levels of resource density (N_R) and social learning (α) over 500 simulations. Index values greater than 1 imply that the mutant μ will be over to invade the resident μ and are represented by red hues.

4.4.2 High levels of aggregation increased payoffs from exploratory strategies and decreased the likelihood of exploiters invading populations.

To understand the effect of competition on the search strategies, we considered a case of large group size ($N_A = 50$) under different levels of social learning. High levels of social learning ($\alpha = 10^{-5}$) in large groups can cause agents to excessively overcrowd at a patch, lead to a rapid depletion of patches and decrease the likelihood of finding resources soon after its discovery. Under such conditions of high competition, we found that rapid exploitation of patches led to higher payoffs for fast explorative strategies ($\mu \to 1$) that could not only increase the rate of discovery but also help the 'producers' exit the patch quickly to maximize their returns before others joined. In addition, in larger groups, the higher number of exploratory agents likely increased the rate of resource discovery and thus, further increased the payoffs from fast explorations. Due to this, we observe that strategies $\mu \approx 1.1$ are not likely to be invaded by other strategies, especially by exploitative ones (Figs. 4.4, 4.1).

The advantage of highly explorative strategies further increased in richer patches, contrary to the effect we noted in small groups. As explained in the last chapter, the chances of 'snowballing' or excessive aggregation of agents on a patch increase in large groups that are further amplified in rich patches due to longer patch-residence times. Therefore, under extremely high competition, exploratory strategies which find a patch before anyone else and exit it before others arrive gain higher payoffs, and exploitative strategies that arrive later to a patch receive lower payoffs.

However, when agents are selective social learners, the aggregation and subsequent competition at patches decreases, and the average values of μ shift towards slightly larger values. In addition, exploitative strategies receive a higher payoff, and highly explorative strategies' payoffs decrease compared to the minimally-selective case. Thus, as explained in the previous section, this effect leads to a mixed ESS where explorative and exploitative strategies can regularly invade each other. However, in large groups, the likelihood of exploiters invading explorers is less than in small groups and further decreases in richer patches.



(a)

(b)

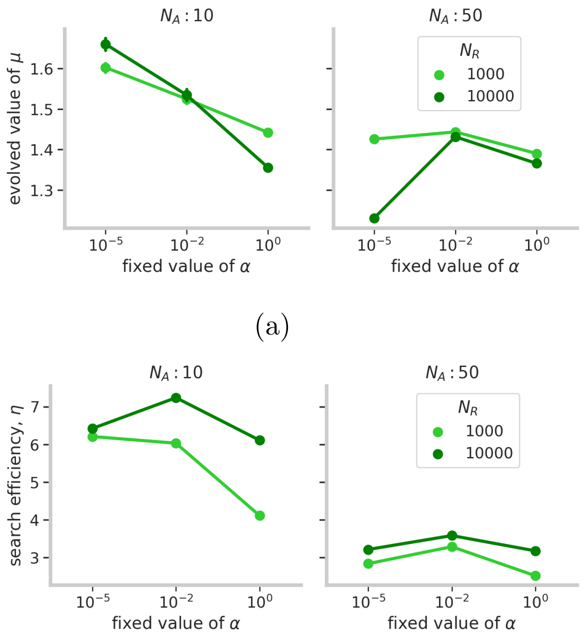
Figure 4.5: ***(a)*** Mean estimates of the evolved values of Lévy exponents (μ) for different levels of resource density (N_R), group size (N_A) and social learning (α). ***(b)*** Corresponding mean estimates of the group search efficiencies (η) of the evolved groups. Dashed lines show the maximum group efficiency value obtained in the last chapter for a particular parameter combination. The averages were taken over the last 10 generations out of a total of 3000, for every parameter combination.

4.4.3 Selective social learning decreased payoffs from exploiting and increased group search efficiency.

In the previous chapter, our results showed that in small groups, group-level search efficiency is maximized with explorative individuals ($\mu = 1.1$) practising high levels of social learning ($\alpha = 10^{-5}$) that was not sensitive to the costs of distance and opportunity associated with following social cues far away. However, in large groups, we had found that such indiscriminate social learning can result in excessive overcrowding at resource patches, and thus, selectivity in pursuing social cues is essential to increase group performance.

Contrary to these results, we found that selective social learning ($\alpha = 10^{-2}$) in the evolutionary model results in groups with maximum group search efficiency, in both small and large groups (Fig. 4.5b). In the results presented above, we showed that in small groups with minimally-selective social learning, exploitative strategies had high payoffs, and evolved groups were composed of exploiters in higher numbers than explorers. Due to the low frequency of explorers, groups faced lower rates of resource discoveries and overall group-level exploration, which in turn diminished group-level search efficiency. We can see in Fig. 4.3 that when groups' mean μ values were high, their search efficiencies decreased.

However, when agents pursued social cues only selectively ($\alpha = 10^{-2}$), exploitative agents had to resort to independently searching for resources and bear high search costs, especially in scarce conditions, which decreased the proportion of exploitative agents, and increased group efficiencies. On the other hand, in large groups, the higher group search efficiencies in selective social learning conditions were not driven by high proportions of exploratory individuals. By contrast, evolved groups in the $\alpha = 10^{-5}$ condition were more explorative than in the $\alpha = 10^{-2}$ condition. However, the overall levels of independent exploration practised by agents were lower when they readily and excessively pursued social cues than in the selective condition. Further, selective social learning allowed simultaneous discovery of multiple resource patches and thus, reduced overcrowding at patches and increased group search efficiency. Taken together, our results suggest that groups can improve their collective efficiencies when



(a)

(b)

Figure 4.6: ***(a)*** Mean estimates of the evolved values of Lévy exponents (μ) from the area-restricted search 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.

exploratory strategies have higher payoffs than exploitative strategies. To further test this effect, we modified the model to include area-restricted search, which we hypothesized could increase the payoffs for exploratory agents and lead to the evolution of more efficient groups.

4.4.4 Area-restricted search increased the payoffs from exploratory search and increased group search efficiency.

The addition of an area-restricted search component to the model had several consequences for the foragers. First, it added informed movements to an agent's search behavior and, thus, decreased search costs associated with random movements. As a consequence of this, the overall search efficiencies of the strategies increased (Fig.

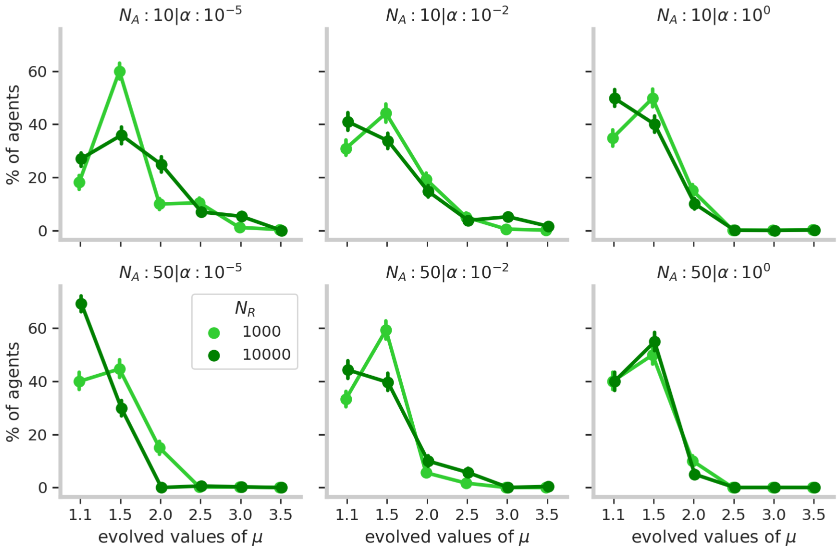


Figure 4.7: Distribution of the evolved values of Lévy exponents (μ) for different levels of resource density (N_R), group size (N_A) and social learning (α). These data represent group compositions over the last 20 generations out of a total of 3000.

B.1) for all values of μ and α. In contrast to the results from the previous chapter, which showed that $\mu = 2$ is more efficient than $\mu = 1.1$ when there was no social learning involved, we found that for ARS foragers, $\mu = 1.1$ is better than $\mu = 2$ even without any social learning. This effect is due to the fact that $\mu = 1.1$ in ARS foragers resulted in trajectories that adaptively switch from short, exploitative bouts to straight-line, explorative movements only if there are no resources in their vicinity.

Secondly, it increased the payoff from discovering an undepleted patch farther from others because ARS foragers were better at sensing resources at a patch than non-ARS foragers, who needed others to be present at the patch in order to sense and harvest the resources efficiently collectively. This effect also increased the time agents, even the exploratory ones, spent at a resource patch, and in turn, could cause stronger overcrowding than in the non-ARS case and increase competition between agents due to faster rates of patch depletion. As a result, the payoffs from exploitative strategies decreased drastically, and explorative strategies could resist invasions from exploiters. We can see that the average μ values decreased closer to 1.1 (Fig. 4.6a), and the evolved composition of the groups had a far lesser proportion of exploiters than in the non-ARS model (Fig. 4.7). However, as noted in the previous sections, the degree of exploration or the proportion of explorers in the evolved groups depended upon patch-richness, social selectivity, and group size. For instance, the average μ in small groups with selective social learning was lower than with minimally-selective social learning. Unlike in the non-ARS model with selective social learning, the proportion of extreme explorers ($\mu = 1.1$) was larger. This effect can be explained by the increase in the patch-residence times of $\mu = 1.1$ due to ARS behavior, which allows the agents to exploit the patch before exiting it. We also found that the mean efficiencies were also higher in the ARS model (Fig. 4.6b), and the difference between solitary and collective foraging was smaller than in the ARS model, especially in conditions with rich patches. Because resources were densely clustered together in the rich conditions, ARS was a more effective strategy, and individual agents could efficiently sense and exploit a patch.

4.5 Discussion

Many previous works have studied search strategies that an individual forager should adopt to optimize its search efficiencies and maximize its fitness (Charnov, 1976; Viswanathan et al., 1996; **?**). Nevertheless, in many cases, search or foraging occurs in groups where multiple foragers collectively search for resources and share the information about their findings with each other. However, how individual search strategies evolve in group foraging and which strategies maximize individual and group fitness has been understudied. In this chapter, we develop an evolutionary model of collective foraging where individual search strategies are selected in proportion to their search efficiencies under different physical and social environments. We further investigate whether the evolved individual strategies maximize mean group fitness or not, and test how heuristics like area-restricted search can improve both individual and collective efficiencies.

Foraging efficiency is determined by how well individuals can locate a resource and whether they can optimally switch from exploiting a patch before facing diminishing returns to exploring for new patches. In collective foraging, individuals can integrate obtained by each other to efficiently find and exploit resource patches (Giraldeau, 1984), and increase their individual and group-level fitness. However, excessive grouping and social learning between individuals can decrease overall exploration for better resource patches or solutions. Further, at the individual level, it can increase competition for resources, cause exploitation of others findings, and prompt foragers to modify their strategies to accommodate such pressures. The last chapter showed that high levels of exploration could increase group efficiencies in social learning populations by helping groups discover new resource patches more efficiently. Our results in this chapter show that individuals may not always evolve highly explorative search strategies.

We found that when competition and aggregation at patches was not too high, for example in small groups, exploitative agents could sufficiently gain from exploiting a patch found by explorers and increase in population, but at the expense of mean group efficiency. This effect prevented groups from being composed of only explorative or exploitative agents, and instead they were composed of a mix of explorative and exploitative agents. Further, the balance between explorative and exploitative strategies in the evolved groups was affected by the patch richness, where exploitative agents were higher in number in richer patches (Caraco and Giraldea, 1991). However, when groups were larger and many agents aggregated at resource patches, increased competition substantially decreased the payoffs from exploitative strategies, and increased the payoffs from highly explorative strategies. Consequently, populations evolved to be primarily composed of explorers who were quick to exit a patch quickly before facing diminishing returns due to excessive aggregation.

We also found that the benefits of explorative strategies could be further amplified when agents could practise area-restricted search, which allowed them to exploit a resource patch effectively before exiting it. Due to the non-random exploitation of patches, we found that ARS decreased the relative advantage of collective foraging, increased foraging efficiencies and the payoffs from discovering undepleted patches. Moreover, our results show that such heuristics can help maximize both individual and collective foraging efficiencies. This effect is similar to that of finder's advantage or producer's share described in producer-scrounger models, where if producers gain a large share of a patch they discover, they are less likely to be invaded by scroungers (Di Bitetti and Janson, 2001). Based on our results, we suggest that simple heuristics like ARS that have been noted in many animals and humans (Pacheco-Cobos et al., 2019; Wiesner et al., 2012) can help maintain explorers in a population and increase individual and group efficiencies in environments with clustered resources.

Our model is similar to the classic producer-scrounger models where agents can either independently search to find new patches or use social information to scrounge the patches discovered by producers (Barnard and Sibly, 1981; Caraco and Giraldea, 1991), and neither strategy can invade the other under many circumstances resulting in a mixed ESS. However, in our model, the difference in producer and scroungers arises due to the differences in the rate of patch discovery, where explorative agents ($\mu \leq 2$) are more likely to discover new patches and thus act as producers. In contrast, exploitative ones ($\mu > 2$) are less likely to find patches independently and resort to scrounging. Our results thus highlight that producer-scrounger dynamics can emerge due to differences in exploration speeds even in populations where every individual practises social learning.

In addition, our model's spatially-explicit framework helps consider the effect of competition, which is often discounted in the PS models that generally assume that a patch is consumed almost instantaneously after being located. PS models and related studies have shown that an increase in group size decreases the proportion of producers because of reduced finder's advantage (Coolen, 2002; Dumke et al., 2016; Vickery et al., 1991) and increases the number of scroungers due to increased opportunities to scrounge (Aplin and Morand-Ferron, 2017). In contrast to these predictions, we found that an increase in group size increased the relative payoffs from exploratory strategies and the proportion of explorers. In our model, an increase in group size increased the overall use of social information and intensified the competition and the penalty for the late-arriving scroungers. Moreover, an increase in group size accelerated the rate at which resource patches are discovered and, thus, further increased payoffs from exploratory strategies that quickly exit a patch.

Similar to the predictions from PS and social learning models, we also found that a decrease in payoffs from exploratory strategies depresses group-level search efficiencies

(Caraco and Giraldea, 1991; Rogers, 1988). Exploiters in our model had meager rates of resource discoveries and overlapped with each other in the space they searched, thus diminishing mean group fitness. By contrast, as shown in the last chapter, high levels of independent exploration in groups with social learners maximized search efficiencies by reducing overlap in search areas and a high rate of resource discoveries. In line with predictions with social learning models, we found that selective social learning, where individuals filter out costly and distant social cues, increased group efficiencies. However, our results suggest a different mechanism behind this relationship: in our model, selective social learning decreased the probability of social learning and thus reduced the payoffs from exploitative strategies, promoted exploratory strategies, and increased group fitness.

Many previous studies have shown consistent differences in exploratory behavior between individuals in groups. Our model suggests that these differences may not always be adaptive, and a high proportion of exploiters can decrease the mean fitness of a population. However, in many natural conditions, explorative strategies may have additional risks (such as predation or high search costs) 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 explorative strategies that continue searching for better options would be selected against (Arbilly et al., 2011). In addition, if the tendency to explore is negatively associated with the likelihood to socially learn (Kurvers et al., 2010), then groups would benefit from a mix of asocial explorers that find resource patches and social exploiters who harvest a found patch. It would be interesting to test the effects of costly and risky exploration, and the association between exploration and sociality by extending the current model. Further, individual differences in the degree of exploration or boldness may be necessary for coordination in movement and decision-making in groups (Johnstone and Manica, 2011; Jolles et al., 2015; Kurvers et al., 2009).

In conclusion, the present work studies the evolution of explorative and exploitative search strategies in collective foraging and shows how the differences in exploratory speed can form the basis of various behavioral syndromes like producer-scrounger. We further highlight the role of physical and social environments in determining the costs and benefits of exploratory and exploitative strategies, the resultant composition of foraging groups and their mean efficiencies. Moreover, we show that strategies like area-restricted search can increase explorers' payoffs and consequently, group efficiencies.

Different social systems may employ other mechanisms to maintain explorers or producers in a population, for example, patents, social prestige, synchronized food-sharing in hunter-gatherers (Giraldeau et al., 2017; Winterhalder, 1996). Future models can compare the effect of these different mechanisms on the evolution of search strategies. Future models can also study the evolution of social learning strategies as a factor of search strategies or the co-evolution of social learning and search strategies under different contexts to shed light on the interplay between search behavior and sociality.

Chapter 5

Modeling hunter-gatherer social networks from individual-level foraging and movement patterns

5.1 Preface

In the final study of this dissertation, I present work that offers a different yet related perspective on the effect of individual-level foraging behavior on group-level behavior under various environmental factors. In mobile organisms, movement patterns are one of the key factors that influence how they socially interact with each other. Over the course of our evolutionary history, movement driven by foraging likely played a significant role in shaping the social interactions of our ancestors and subsequently, their social networks and group-level behavior. In this study, we simulate hunter-gatherer foraging behavior and under different environmental conditions, we test whether movement patterns generated from such behavior could have resulted in social networks that positively affected our species' social and cultural abilities. We build an agent-based model of central-place foraging, where foragers return to a central location (or home) and periodically move their homes to other locations. The agents foraged within a given radius or moved their home to another location according to a simple optimal foraging rule, and could encounter other agents as they moved across the space. We analyzed the interaction networks arising under different conditions, and found that, at intermediate levels of environmental heterogeneity and mobility, central-place foraging increased global and local network efficiencies as well as the rate of contagion-based information-transmission. We also found that central-place mobility strategies can further improve information transmission in larger populations. Our findings suggest that the combination of foraging and movement strategies, as well as the environmental conditions that characterized early human societies, may have been a crucial precursor in our species' unique cultural abilities to collectively search for solutions.

5.2 Introduction

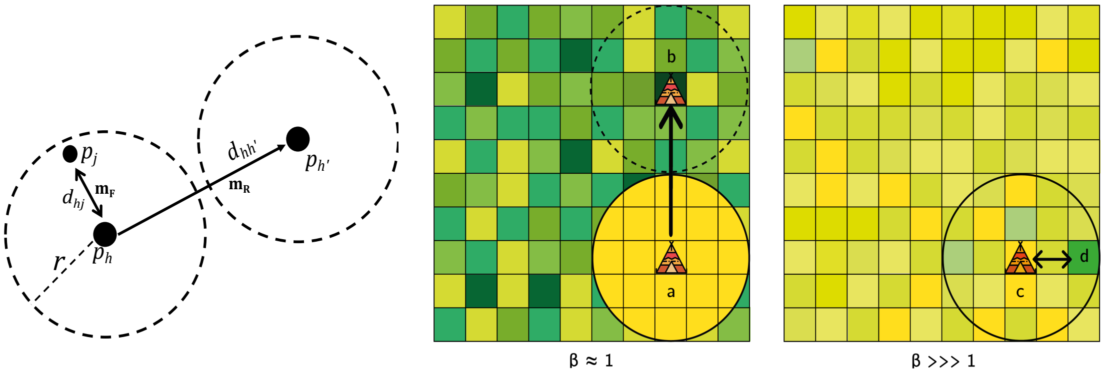
One of the pivotal transitions in human evolution is our ability to generate, accumulate and rely on complex, cumulative culture (Derex and Boyd, 2016b; Hill et al., 2011, 2014; Muthukrishna et al., 2014). Recent evidence from hunter-gatherer societies (Migliano et al., 2017, 2020) suggests that changes in our ancestors' social networks and connectivity could have promoted such a transition by facilitating an efficient exchange and transmission of cultural information. Given that the frequency and nature of social interactions between hunter-gatherers would have been affected by their movement and spatial distribution patterns, researchers have proposed that divergences in foraging behavior, coupled with ecological changes, could have led to changes in the dynamics of social interactions and hence patterns of social organization (Dyble et al., 2015; Foley and Gamble, 2009; Kuhn, 2020). However, the impact of hunter-gatherer foraging and movement behavior on emergent social networks and their ability to transmit information is still not thoroughly understood (but see Premo2015, Dyble2018).

Central-place foraging marks a critical behavioral change between the foraging styles of early hominins and our closest great ape relatives that would have modified their movement and consequently spatial and social patterning (Isaac, 1978; Layton and O'Hara, 2010; Marlowe, 2005). Non-human Great Apes (henceforth Great Apes) tend to consume food when they find it ('point-to-point' foraging), make sleeping nests at variable locations and have short foraging trips (Jang et al., 2019). On the other hand, hunter-gatherers establish residential camps or central places around which they systematically forage and bring the food they collect during foraging trips (or logistical forays) back to their camps to share and process it with camp members ('central-place' foraging) (Binford, 1980; Kelly, 1983). In addition, human foragers can make longer foraging trips and periodically move the location of their residential camps to access new resource areas with little overlap in the foraging-radii between successive camps. These properties result in an expansion of their overall home-ranges during their lifetimes (Jang et al., 2019) compared to other primates who spend most of their adult lives within the same area, leading to a more restricted use of space (Herbinger et al., 2001; Kelly, 2013; Kouakou et al., 2011; Marwick et al., 2003; Povinelli and Povinelli, 2001).

Such differences in mobility could have altered spatial patterns and dynamics of social interactions and led to more complex social structures. In particular, we hypothesize that central-place foraging could have played an essential role in the subsequent development of multi-level sociality. In multi-level organizations, sets of multiple core units (such as nuclear families) repeatedly coalesce, intermix and disperse, giving rise to relatively fluid local bands that are embedded in higher-level interconnected regional networks(Bird et al., 2019; Grove, 2009; Grove et al., 2012a; He et al., 2019; Layton and O'Hara, 2012; Romano et al., 2020). These extended, flexible, and fluid social landscapes would have increased the likelihood of interactions, and consequently opportunities social learning, and information exchange compared to the rest of the Great Apes (Grueter and White, 2014; Hill et al., 2014).

However, hunter-gatherer foraging and mobility decisions (e.g. daily trips, residential movements) are influenced by their resource environments as well as various costs (e.g., traveling costs) and benefits (e.g., resource abundance) of their foraging activities (Pacheco-Cobos et al., 2019; Winterhalder, 1981). For example, in rich environments where there are plenty of resources available within their foraging-radii (or home-ranges), hunter-gatherer bands may be able to afford greater sedentism (Hamilton et al., 2018b). In contrast, unproductive landscapes may require bands to move their camps multiple times a year due to resource depletion within their foraging radii (Venkataraman et al., 2017). In addition, if resources are homogeneously distributed, ethnographic studies have shown that bands tend to predominantly rely on short and frequent residential moves (Binford, 1980). In these settings, the frequency of encounter with other bands and thus, the inter-connectivity between them could decrease. Conversely, if resources are heterogeneously distributed and some areas are more resource-rich than others, bands may aggregate in key locations from which they conduct daily trips to procure resources (Winterhalder, 1981), potentially generating more opportunities for interactions (Henrich, 2004).

In this chapter, we model and compare point-to-point and central-place foraging (with different home-range radii) behavior across a range of environments. We investigate the effect of central-place foraging and mobility on the interaction patterns between foraging units and the subsequent social networks that are formed due to foraging units coinciding on resources. We then test the efficiency of information transmission in the networks that emerge from the different mobility regimes and environments. Previous theoretical and computational models have explored the effects of environmental heterogeneity on social networks emerging from foraging behavior across different environments (Ramos-Fernández et al., 2006) and hunter-gatherer mobility on cultural transmission (Perreault and Brantingham, 2011; Premo, 2015). However, models explicitly linking foraging strategies, environmental features, and hunter-gatherer interaction networks remain lacking. Our work illustrates a direct connection between environmental conditions, foraging behavior, and information flow in hunter-gatherer social networks, thereby providing insights into the evolutionary origins of our species' unique ability to innovate, accumulate and rely on complex culture.



(a)

(b)

Figure 5.1: Model Description. ***(a)***: A schematic representation of agent movement in the model. Agents can make foraging movements (m_F) within a radius r from their home (p_h) to a new patch (p_j) or residential movements (m_R) to a new home ($p_{h'}$). ***(b)***: An illustration of the variations in resource environments modulated by the parameter β. A low value of β results in a rich (dark-green patches) and heterogeneous environment (left), whereas a very high value of β results in a scarce (yellow patches) and homogeneous environment (right). When food depletes within an agent's radius (yellow patches), it moves its residence ($a \rightarrow b$). Otherwise, it continues to forage within its radius ($c \leftrightarrow d$).

5.3 Methods

5.3.1 Model Description

We investigated how central-place-foraging behavior would affect the emergent interaction networks across environments. Previous work by Ramos-Fernández et al. (Ramos-Fernández et al., 2006) modeled the effect of environmental heterogeneity on the interaction networks that emerge from multiple agents foraging independently (representing spider monkeys). The authors showed that a complex social structure with fission-fusion properties, resembling those observed in field studies among real spider monkey societies, could emerge simply from optimal foraging rules in heterogeneous environments.

Our model (henceforth central-place model), like the model from Ramos-Fernández et al. (Ramos-Fernández et al., 2006) (henceforth point-to-point model), was executed in a two-dimensional environment spatially ranging from 0 to 1, and comprising 50,000 uniformly distributed patches. Each patch was initially assigned resource content, $k_i \geq 1$, drawn from a normalized power-law probability distribution, $P(k) \approx Ck^{-\beta}$ where the exponent β determined the distribution of resource content and the total resource abundance, and $C = 1/\sum_{k=1}^{\infty} k^{-\beta}$ was the normalization constant. Following this equation, the richness of an environment (or abundance) and its heterogeneity (or distribution) co-varied and were determined by β.

When $\beta \approx 1$, k had a broad range with high values, patches varied widely in their resource content, and the environment was abundant with many rich patches. Conversely, $\beta \gg 1$ corresponded to smaller values and a restricted range of k that resulted in an environment composed of scarcer resources that are homogeneously distributed across patches. Patches were depleted by a unit in their resource content (k) every time-step that a foraging-unit spent at it, and they did not regenerate (see Fig. C.1 for more information on resource depletion).

Each agent in our simulation represented a monogamous, nuclear family/foraging unit (adult male, female and dependent offspring) which are the core, indivisible units of social organization across hunter-gatherer societies (Lewis et al., 2014). Since ties between individuals from different families would result in a tie between the families, agents were assumed to forage and move as a single foraging-unit. The model was initialized with agents independently and randomly distributed across the patches. Foraging-units followed a rule whereby they move to a new patch (p_j) from a depleted patch (p_i) such that it minimized the cost/gain ratio (d_{ij}/k_j), where d_{ij} is the distance between the patches and k_j is the resource content of p_j. Our model (Fig 5.1a) modified this resource-maximization rule to implement central-place foraging and distinguished between foraging (or logistical) and residential moves (Binford, 1980; Kelly, 1983).

In our model, foraging-units moved to fixed home locations from which they exploited the surrounding local environment in their foraging radius before moving to another home location. Every foraging-unit had a complete knowledge of resources, a randomly allocated home location (i.e. central place), and a foraging area with a given radius, r. Foraging-units could forage and change their home location based on the following rules: When foraging-units were on a patch with no food left, they made foraging moves (m_F) to a patch (p_j) within r such that the cost/gain ratio (d_{hj}/k_j) was minimized, where d_{hj} is distance from the current home (p_h), and k_j is the resource content of p_j (Fig 5.1b (right)). Before every move, foraging-units compared the cost/gain ratio of patches outside the radius to patches within the radius. When the resource quality within r diminished compared to the rest of the environment (Fig 5.1b (left)), instead of making a foraging move to profitable patches outside their radius, foraging-units made a residential move. Residential moves (m_R) allowed foraging-units to select a new home ($p_{h'}$) that minimized ($d_{hh'}/k_{h'}$) but was far enough from the current base ($d_{hh'} \geq 2 * r$) to avoid overlap (Premo, 2015). Each time-step that a foraging-unit coincided with another foraging-unit on a patch, they formed a social network tie or added a unit of weight to an existing tie. This can therefore be considered to represent a tie between two core family units. In the literature, hunter-gatherer family units have been well-documented to regularly interact, fuse and disband to form a higher level of organization (bands or camps), which our model simulates (Binford, 1980; Kelly, 2013; Migliano et al., 2017, 2020) . At the same time, such bands have been shown to share the same home-bases (or central places) and often co-reside. In our model, when two family-units coincide on a home-patch, they share the same home range and forage together. In contrast, if two foraging-units share a foraging-patch (as opposed to a home-patch), they will have overlapping home ranges which can also increase the likelihood of interactions and result in larger communities (Hamilton et al., 2007, 2018a).

To assess how the combination of environmental heterogeneity and central-place foraging strategies affect the emergent social networks, we varied the resource exponent, β parameter to take values between 1.5 and 4.5 and the foraging radius, r to assume values of 1, 0.1, 0.01, and 0.001. We ran the point-to-point model by setting the radius to 0 after verifying this was equivalent to the framework from Ramos-Fernández et al. (Ramos-Fernández et al., 2006). We also tested the effect of population size by running the model with 50, 100, and 200 foraging-units. Whilst our main motivation with this manipulation was to explore the effect of changing population sizes on our model results, the values we chose are ethnographically meaningful. We mostly focused on population sizes of 100 foraging units/families (that correspond to 500 individuals) which have been widely documented (Steward, 1968) and are assumed to represent the average size of hunter-gatherer regional bands or groups (Kelly, 2013). Populations of size 200 correspond to prevalent estimates of the size of entire ethnic populations (or metapopulations) (as compiled in Lehmann et al. (Lehmann et al., 2014)). Finally, populations of 50 families (200-250 individuals) represent of a lower limit for hunter-gatherer populations to remain viable (Wobst, 1974). We ran 50 simulations for each parameter combination and the point-to-point model and extracted the weighted social networks formed throughout the simulation as well as at the end of the simulation. To ensure that our results are not an artifact of the chosen time-steps, we conducted sensitivity analyses, running each parameter combination for 1000 time-steps (see Appendix). We found the results to be consistent over longer time-steps and thus, report the results from the first 100 time-steps in the following text.

5.3.2 Networks

We extracted the final networks formed from the sum of all interactions by the end of each run. As a robustness check (Appendix C), we also looked at how the networks developed across the simulations. For 100 time-steps, we examined the networks after each interval of 10 time-steps. For 1000 time-steps, we increased that window to a 100 time-steps.

Efficiency

We tested the networks for their ability to transmit information by measuring their global and local efficiencies (Latora and Marchiori, 2001). The efficiency measures have been used across various studies to investigate the transmission of social and cultural information in various networks, including hunter-gatherer social networks (Migliano et al., 2017). Global efficiency indicates a network's ability to transmit information across the entire network and is inversely related to the characteristic path length (or the average distance between nodes). Latora and Marchiore (Latora and Marchiori, 2001) define a graph's global efficiency as the inverse of the sum of the shortest paths between all nodes i and j:

$$E = \frac{1}{n} \sum_{i \in N} \frac{\sum_{j \in N, j \neq i} d_{ij}^{-1}}{n-1} \tag{5.1}$$

Where N is the set of all nodes in the network, n is the total number of nodes, and d is the shortest distance between two nodes. On the other hand, local efficiency relates to the clustering coefficient of a network (i.e., the degree to which a node's local neighborhood is inter-connected). It measures the average global efficiency of subgraphs and denotes how well each local neighborhood can exchange information within itself. We modified the efficiency measures to incorporate weights (for a more detailed description, see Appendix C).

Contagion simulations

We conducted contagion simulations on the extracted networks, and calculated the proportion of agents that acquired the diffusing information. Each simulation consisted of 5000 time-steps and we conducted 50 simulations on each network to account for variation across runs. For each simulation, we randomly chose one agent and seeded it with the behavior to be transmitted. As the simulation proceeded, other agents adopted the behavior with a probability proportional to the number of their neighbors that had already acquired it and the strength of their ties with them. However, the way this probability was calculated varied for simple and complex contagion, and we explored both conditions in our analyses. Simple contagion models a transmission where the probability with which an agent ($Pr(A)_i$) acquires information is dependent upon the strength of ties and number of neighbors with the information. This can be expressed as :

$$Pr(A)_i^{t+1} = \frac{\sum w_i \times d^t}{\sum w_i}$$

Where w_i is a vector of the edge weights that i shares with its neighbors and d is a vector of same length containing 1 if the corresponding neighbor has acquired the information or 0 otherwise at time, t.

To illustrate, consider that the agent, A_i has 3 neighbors (A_j, A_k, A_l) and the ties with them have different weights (2, 5, 10). If A_l has information then the probability of A_i acquiring it ($P(A_i) \approx 0.59$) is higher than if A_j had information ($P(A_i) \approx 0.12$).

We also modeled a more restricted mode of transmission (complex contagion) that increases the dependence on how many of an agent's neighbors have the information and the strength of their ties. Complex contagion is more suited to capture the diffusion of costly or difficult behaviors that are socially acquired (such as cultural traits) and need reiterated affirmation (Centola, 2010; O'Sullivan et al., 2015). Here, the probability of acquisition now rises exponentially as more neighbors acquire the information:

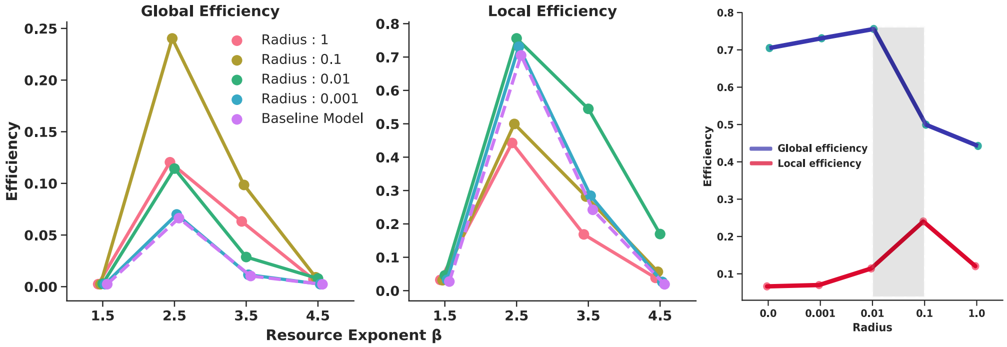
$$Pr(A)_i^{t+1} = \left(\frac{\sum w_i \times d^t}{\sum w_i}\right)^2$$

Given this type of contagion, the probability of A_i acquiring information from A_l reduces to $P(A_i) \approx 0.34$ and thus, stronger ties and more neighbors with the information would be required to increase the likelihood of transmission.

5.4 Results

5.4.1 Environmental factors affect the efficiency of information transmission in networks

In line with the results from Ramos-Fernández et al. (Ramos-Fernández et al., 2006), we found that environmental heterogeneity strongly influenced the networks formed, with $\beta = 2.5$ generating the most efficient networks ($\overline{E}_{global} = 0.13, \overline{E}_{local} = 0.65$). In environments of ($\beta \approx 1$) where many rich resource patches were available, foraging-units had very low mobility (see next section for mobility results) and stayed fixed at a rich resource patch for long durations. In the homogeneous environment of $\beta = 4.5$, every patch had low resource value, and foraging-units depleted patches



(a) (b)

Figure 5.2: Network Efficiencies after 100 time-steps. (a) The plot shows the average global (left) and local (right) efficiencies of the networks as a function of environmental heterogeneity for each radius. (b) The plot shows the relationship between efficiencies and radius for $\beta = 2.5$. Shaded region corresponds to intermediate radii that balances global and local efficiencies.

quickly. They frequently moved across the environment resulting in low interaction rates (as evidenced by density of connections) with other foraging-units. However, at intermediate heterogeneity and resource abundance ($\beta = 2.5$), foraging-units coincided at many different rich patches available in the environment and formed stronger social ties. This can be evidenced by the high number of total interactions between foraging-units per time-step (Fig. C.2) that increased the network's local efficiency. On the other hand, an intermediate number of rich patches also enabled more movement and unique interactions between the foraging-units that made the network more expansive and increased its global efficiency (Figs. C.8, C.9). Higher population sizes further increased the rate of interactions between the foraging-units and thus, the network efficiencies.

5.4.2 Central-place foraging increases global and local network efficiency

We found that point-to-point foraging created networks comprised of isolated foraging-units with very high local efficiency (or clustering) but low global efficiency. These networks contained strongly connected small sub-groups of foraging-units that were distributed across the environment with few to no connections between them. In contrast, central-place foraging increased the number of unique interactions between foraging-units (Figs. C.8, C.9) and created ties between otherwise unconnected sub-groups (or components) that resulted in a more inter-connected and expansive network (Fig. C.3). A completely disconnected graph has a number of components equal to its nodes, while a fully connected graph has a single component. We found that the ties between sub-groups decreased the number of components and increased networks' global efficiency while maintaining high local efficiency. On the one hand, this formed strongly bonded local groups, and on the other hand, large-scale, interconnected regional networks such as the ones observed among ethnographic hunter-gatherers (Bird et al., 2019; Hill et al., 2014; Migliano et al., 2017; Wiessner, 2002)

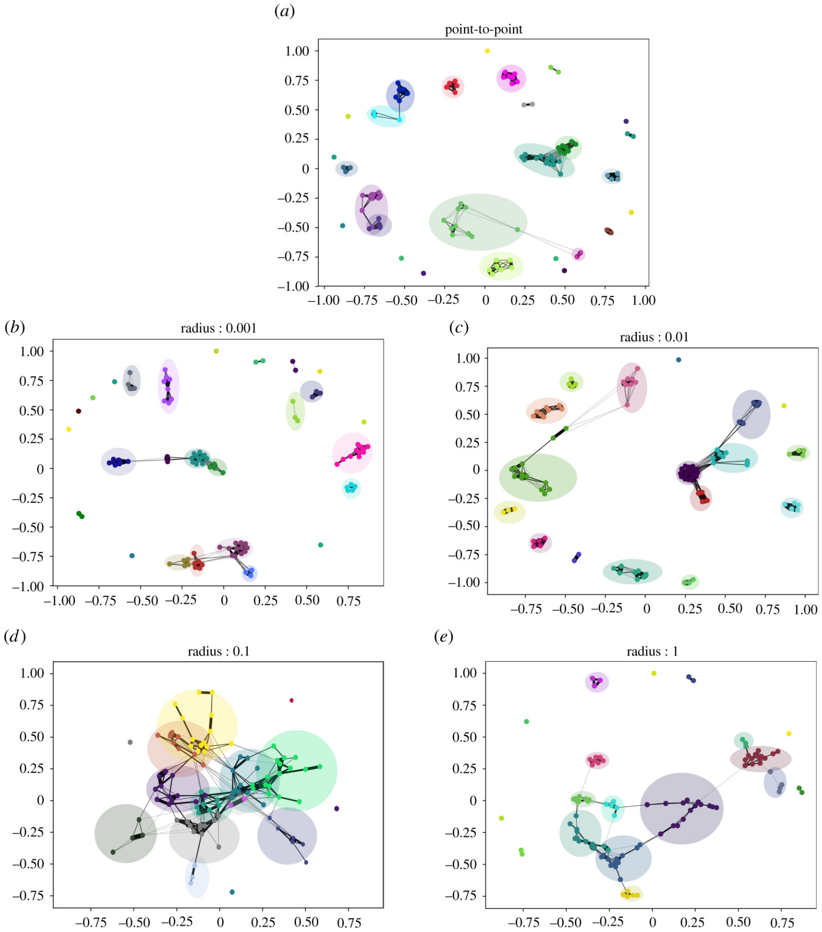


Figure 5.3: Emergent networks from 100 foraging-units after 100 time-steps. The plot shows an example of weighted networks that emerge from different foraging behaviors in $\beta = 2.5$ environment (from (a) to (e): point-to-point, $r = 0.001, r = 0.01, r = 0.1, r = 1$). Node colors depict the different sub-groups detected by Louvain community-detection method (see Appendix C). Different communities and the overlap between them are also shown by circles around each community. Edge widths depict the edge weights, with thicker edges representing stronger bonds, and finer edges representing weaker bonds. Distance between nodes also depict the strength of connections.

To explore the effect of different radii of central-place foraging, we compared the different mobility regimes (frequency and magnitude of residential and foraging moves) across environments and radii (Fig.5.4).

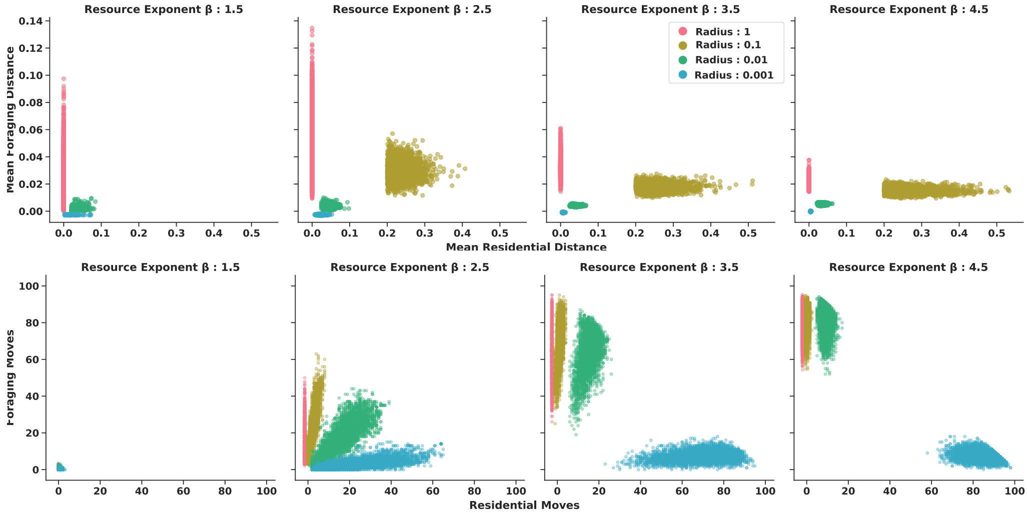


Figure 5.4: Mobility regimes across different environment and radii. ***Top***: The plot shows the mean distance moved in residential moves (d_r) against foraging moves(d_f). ***Bottom***: The plot shows the frequency of residential moves(n_r) and the frequency of foraging moves(n_f).

When the foraging radius was small ($r = 0.001$), at intermediate levels of environmental heterogeneity ($\beta = 2.5$), the observed foraging pattern closely resembled point-to-point foraging (Jang et al., 2019), where foraging-units don't return to a central-place, make short residential moves ($\overline{n}_r = 26, \overline{d}_r = 0.022$) and fewer and shorter foraging moves ($\overline{n}_f = 3, \overline{d}_f = 0.001$). The resulting networks from $r = 0.001$ comprised many (≈ 24) densely connected sub-groups of high local efficiencies ($\overline{E}_{local} = 0.73$). Nonetheless, these dense sub-groups lacked connections between them with a maximum of 3 sub-groups connected to each other.

Increasing the foraging radius to intermediate values ($r = 0.01$ and $r = 0.1$) resulted in foraging-units making longer, and more frequent foraging moves combined with longer but fewer residential moves. At $r = 0.01$, a small increase in residential mobility ($\overline{n}_r = 16$, $\overline{d}_r = 0.048$) created a few longer connections between the dense sub-groups. These connections resulted in more sub-groups being connected ($4 - 5$) and a more expansive network that increased the global efficiency ($\overline{E}_{global} = 0.11$). However, the network still remained highly cliquish with high local efficiency ($\overline{E}_{local} = 0.75$).

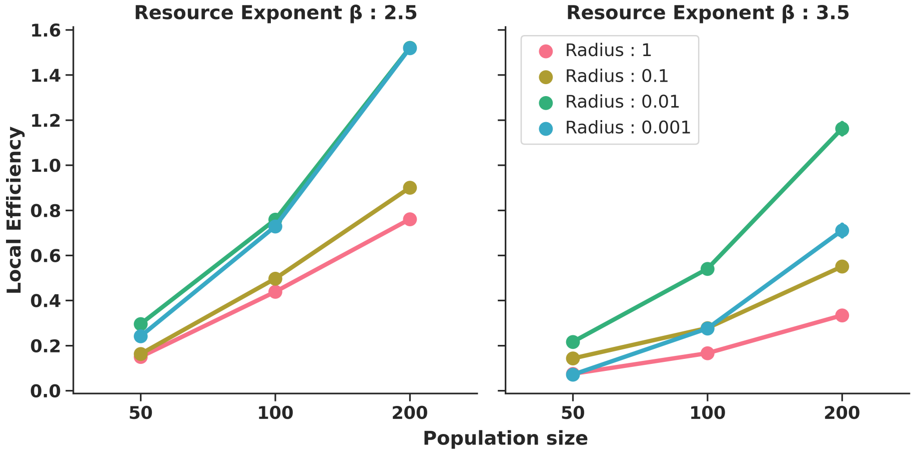
As the foraging radius and use of space further increased ($r = 0.1$), foraging-units moved less frequently ($\overline{n}_f = 20$, $\overline{n}_r = 2$) but undertook longer moves ($\overline{d}_f = 0.03$, $\overline{d}_r = 0.23$). This change in mobility increased the long-range connections between fewer (≈ 15) but larger and interconnected sub-groups ($6 - 8$). The resultant sub-group structure made the network substantially more efficient at the global scale ($\overline{E}_{global} = 0.24$) while maintaining considerable local efficiencies ($\overline{E}_{local} = 0.50$). However, we found that both efficiencies decreased compared to intermediate radii ($\overline{E}_{local} = 0.44$, $\overline{E}_{global} = 0.12$) when the foraging-units had a very large foraging radius ($r = 1$). In the absence of residential moves, the foraging-units remained tethered to their original home and traversed longer foraging moves ($\overline{d}_f = 0.05$) to find food. The longer moves helped create long-range connections between foraging-units that resulted in a large number of connected sub-groups ($7 - 11$) and a more globally efficient network than the point-to-point model ($\overline{E}_{global} = 0.07$). Nonetheless, the strong tethering decreased the overall use of space and the probability of coinciding with others for longer durations, resulting in fewer and weaker connections between sub-groups with low local efficiencies.

In environments where the habitat quality was lower and patches were more homogeneous in their resource content, foraging-units coincided on patches less frequently and for a shorter amount of time, which resulted in fewer interactions. At $\beta = 3.5$ when fewer patches were rich, foraging mobility increased with many shorter moves within agents' foraging-radii for all radii, while residential mobility increased with longer moves ($\overline{n}_r = 2$, $\overline{d}_r = 0.56$) for $r = 0.1$, but decreased for smaller radii with shorter and similar number of moves ($r = 0.01$: $\overline{n}_r = 15$, $\overline{d}_r = 0.041$), or shorter and more frequent moves ($r = 0.001$: $\overline{n}_r = 70$, $\overline{d}_r = 0.006$). This effect led to a decrease in both global and local efficiencies across radii ($\overline{E}_{global} = 0.04, \overline{E}_{local} = 0.3$) from $\beta = 2.5$. However, for radius $r = 0.01$, the decrease in the local efficiencies was lesser when compared to the other radii. For $r = 0.01$, foraging-units moved within a space that was small enough to increase the rate of interactions but large enough to find rich patches. When the radius increased ($r = 0.1, 1$) or decreased ($r = 0.001$), foraging-units either traveled longer distances and were dispersed in a larger area or were too restricted in their space use to find enough food and continually changed their residence.

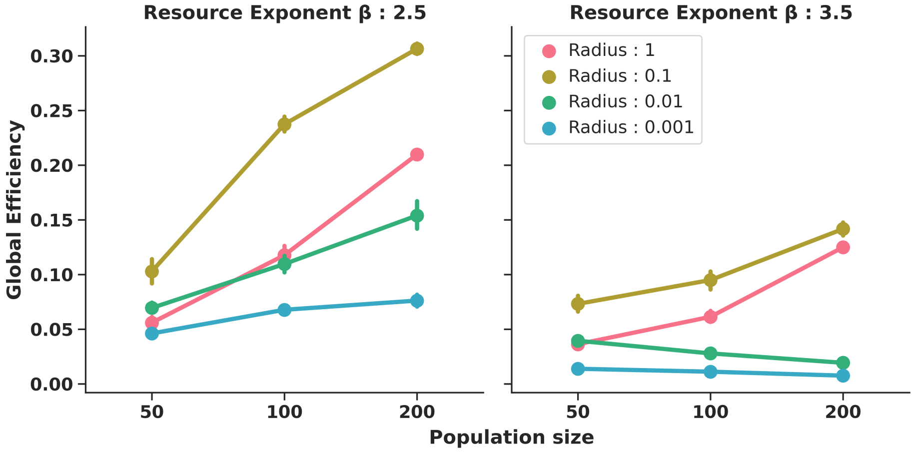
Taken together, these data illustrate that central-place foraging-units were restricted in their movements, which in turn led to strongly connected sub-groups. However, the longer residential moves allowed connections to form between the such sub-groups to varying extents, whilst this was not possible in the point-to-point model. We found that intermediate levels of overall mobility ($\overline{n} = 23$, $\overline{d} = 0.04$) with few long moves and many shorter moves, for example in $\beta = 2.5$ and $r = 0.1$, created networks that were efficient at both global and local scales. As the frequency of overall movement decreased with longer moves($r = 1, \beta = 2.5 : \overline{n} = 15$, $\overline{d} = 0.05$) or increased with shorter moves ($r = 0.01, \beta = 2.5 : \overline{n} = 34$, $\overline{d} = 0.02$; $r = 0.001, \beta = 2.5 : \overline{n} = 28$, $\overline{d} = 0.02$,), networks lacked dense, long-range connections necessary for global efficiency with either highly locally efficient but fragmented networks or sparsely connected sub-groups. Finally, when rate of mobility was very low (highly frequent but very short moves, or rare and and short moves), for example in $\beta = 1.5$ and $\beta = 4.5$ (all radii), foraging-units rarely interacted with each other, and both global and local efficiencies tended to 0. Altogether, based on our results, we show that central-place foraging with an intermediate radius/mobility regime (between 0.01 - 0.1) maximizes both efficiencies (Fig 5.2 inset). Furthermore, our sensitivity analyses indicate that this result remains robust over longer time-scales (see Appendix C).

5.4.3 Population size and mobility affect network efficiency

We also tested the effect of varying population sizes on the resultant networks by simulating populations of 50, 100, 200 foraging-units. We found that as population size increased, regardless of the radius, the local efficiencies of the networks also increased (Fig.5.5a). An increase in population size led to a higher rate of coincidence between foraging-units on patches that created denser connections. This effect was stronger when the radius was smaller ($r \leq 0.01$) because the agents were restricted within smaller areas, which led to repetitive interactions and added weight to local connections. Moreover, when the environment was more abundant and heterogeneous ($\beta = 2.5$) and agents could spend longer times on rich patches and formed more locally



(a) Local Efficiency



(b) Global Efficiency

Figure 5.5: Network efficiencies as a function of population sizes after 100 time-steps for $\beta = 2.5$ and $\beta = 3.5$. Error bars indicate 95% confidence intervals.

efficient networks.

On the other hand, we found that the effect of population size on global efficiency was not as straightforward (Fig.5.5b). In environments with $\beta = 2.5$, global efficiency increased with an increase in population size. This increase was more exaggerated for central-place foraging ($r > 0.001$) and most substantial for intermediate radius ($r = 0.1$). The longer residential moves enabled more foraging-units to interact and helped create a more connected network. It is also important to note that the networks generated by populations of a small size ($n = 50$) and intermediate foraging-radii were more efficient and connected than networks from large population sizes ($n = 200$) that engaged in 'point-to-point' (or $r \leq 0.001$) foraging.

However, for less abundant and more homogeneous environments ($\beta = 3.5$), the effect of population size was diminished and only in the larger radii ($r \geq 0.1$) did it lead to an increase in global efficiencies. When the radii were small or foraging was similar to 'point-to-point', the foraging-units experienced lower encounter rates due to shorter residential moves. Without an increase in long-range connections which would have decreased the path length between network nodes, an increase in population size (or number of network nodes) decreased the global efficiency (Eq. 5.1) of the networks. When foraging-units moved longer distances and foraged within larger radii, long-range connections compensated for a larger network and maintained global connectivity even as population sizes increased. Overall, our results suggest an important role of mobility strategies in mediating the effect of population sizes on information transmission.

5.4.4 Central-place foraging networks are efficient at information transmission

To directly test the networks for their capability of transmitting information, we conducted both simple and complex contagion simulations on the most globally efficient networks that resulted from each model and parameter combination (Acerbi et al., 2020).

In line with efficiency results (see previous section), we found that central-place

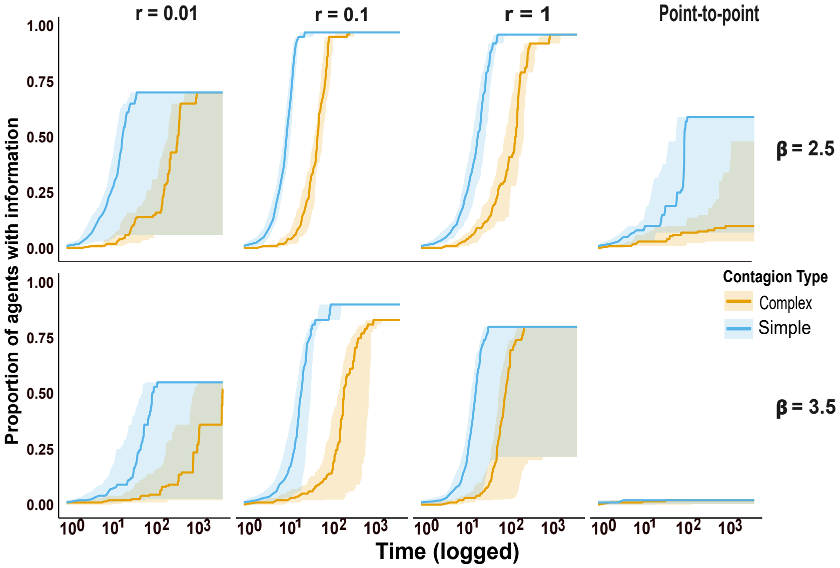


Figure 5.6: Simple and complex contagion trajectories. The plot shows the spread and speed of contagion over time for different radii (columns) and beta (rows). Shaded regions show the 25th and 75th percentiles of the distribution of trajectories at each time-step.

foraging strategies characterized by a combination of residential and foraging moves (e.g. $r = 0.1$ and $\beta = 2.5$) formed networks that allowed a rapid diffusion of information, reaching almost every node. We found that information spread more readily in networks with more extensive and well-connected subgroups when compared to sparser or fragmented networks. For instance, in the point-to-point model, information reached a maximum of around 50% of the population across environments.

In complex contagion, where multiple novel interactions were required for successful transmission of information, we observed a greater effect of network structures and a slower rate of transmission across networks. For example, for $r = 0.1$ and $\beta = 2.5$, simple contagion tended to reach 75% of the nodes much faster and more reliably (± SD) ($\bar{t} = 16 \pm 7$) than complex contagion which took longer time to reach similar proportions ($\bar{t} = 81 \pm 67$). This effect was magnified for less efficient networks (for example, $r = 1$) where the transmission was much slower and more variable ($\bar{t} = 207 \pm 299$) than in simple contagion ($\bar{t} = 33 \pm 16$) to reach the same proportion

(75%) of nodes. In summary, we found that the networks that have high global and local efficiencies (such as those emerging from $\beta = 2.5$ and $r = 0.1$) can maximize both the reach and speed of contagions that resemble cultural transmission.

5.5 Discussion

Recent work on prehistoric and contemporary hunter-gatherer societies has shown that their social networks are efficient at information transmission and could have propelled cultural evolution (Migliano et al., 2017, 2020; Sikora et al., 2017). However, the different factors that could have affected the formation of efficient social connectivity are not well understood. In this chapter, we assessed how hunter-gatherer foraging patterns could have played a role in the emergence of such efficient social networks. We modeled spatial patterns and mobility regimes emerging from central-place foraging, a derived feature in our lineage, under different environments and tested their implications on the emergence of social networks that are efficient at information transmission.

Central-place foraging is characterized by foragers bringing back food to central places (homes) while periodically changing the location of such homes according to the availability of resources. Our results reveal that this foraging pattern under most mobility and environmental conditions could have created social networks that are particularly well-suited for information exchange. Previous works have suggested that a change in spatial and residence patterns could have caused unique expansions in early hominin social networks (Hill et al., 2011; Sikora et al., 2017). We show that, compared to point-to-point foraging, central-place foraging could have modified spatial and residential patterns in ways that would have increased our ancestors' social interactions, made their networks more expansive and improved their ability to exchange information (Marwick et al., 2003). The main finding from the model by Ramos-Fernandez et al. (Ramos-Fernández et al., 2006) showed that interactions between 'point-to-point' foragers following a basic resource-maximisation rule could result in structured networks with fission-fusion dynamics. Moreover, previous works have hypothesized that fission-fusion in non-human primates could have been a precursor for multi-level human social networks (Aureli et al., 2008; Grove et al., 2012a; Grueter et al., 2020; Layton and O'Hara, 2012). Our results show that the addition of central-place foraging can result in a more extensive fission-fusion, larger and more efficient networks, and suggest one possible pathway that could have partly driven such a transition.

We also find support for the idea that environment-driven variability between the mobility regimes employed by different hunter-gatherer societies has significant consequences for their social networks and hence cultural transmission (Collard et al., 2013; Kelly, 2013; Premo, 2015; Read, 2008). Similar to Perreault and Brattingham (Perreault and Brantingham, 2011), we find that mobility regimes which combine short-scale foraging and long-scale residential movements can create more efficient networks as opposed to regimes that are primarily residential or sedentary. In heterogeneous environments, when central-place foragers' movements are restricted within an intermediate radius with occasional long residential moves to richer resource patches, the networks formed contain densely connected sub-groups embedded in more extensive regional networks. Our results predict that an intermediate mobility regime (Fig 5.2 inset), thus, could balance the trade-off between networks that are highly cliquish at the expense of global efficiency and sparser large networks with low clustering. Such networks, similar to small-world topologies, can support information processing at local and global scales (Derex and Boyd, 2016b; Fang et al., 2010; Vining et al., 2019).

In line with previous research highlighting the importance of demography for cultural evolution, we show that, under most circumstances, an increase in population density can result in more efficient networks and a larger capacity for information exchange (Grove, 2016; Powell et al., 2009; Reali et al., 2018). At the same time, we find support for previous predictions that mobility, in addition to population density, plays an important role in affecting cultural transmission (Grove, 2016; Pearce, 2014). We show that residential mobility and central-place foraging can improve connectivity even in small populations (Grove, 2018), and can generate networks that are as efficient as the networks from large populations engaged in 'point-to-point foraging'.

Hunter-gatherer groups with low population densities could have therefore increased their mobility to maintain encounter rates that would have kept them viable by allowing better connectivity, promoting exogamy, efficient exchange of information and resilience to climatic variation (Brooks et al., 2018; Sikora et al., 2017). Thus, our results also emphasize the importance of optimal connectivity and mobility within a population to offset the adverse effects of demographic collapses on cultural transmission (Henrich, 2004; Powell et al., 2009).

Our work reveals that ecologically-driven foraging and mobility decisions can generate networks that resemble the structure and composition of networks observed in real-hunter gatherer societies. The agents or foraging units in our model represented nuclear families which across hunter-gatherer societies normally comprise around 4-5 individuals (Binford, 2019; Lewis et al., 2014). We found that in environments with intermediate heterogeneity ($\beta = 2.5$), central-place foraging with intermediate radii ($r = 0.1$) which afforded local interactions within overlapping foraging-radii and global interactions due to longer residential moves formed networks with multiple and nested levels. More specifically, the emergent networks fused foraging-units into different (≈ 15) sub-groups (analogous to bands of co-residing family units) that were composed of 5-7 foraging-units each, and on an average half of these sub-groups (7 - 9) were inter-connected with sparse ties forming a higher level of organization of ≈ 40 foraging-units (analogous to communities or mega-bands). Such network organization is similar to ethnographic reports across 336 contemporary hunter-gatherer societies (Binford, 2019; Lewis et al., 2014) and estimations based on energetic constraints (Hamilton et al., 2007, 2018b; Kelly, 2013; Marlowe, 2005; Migliano et al., 2017) that show hunter-gatherer regional metapopulations of 100 families that can be fragmented into co-residing bands of ≈ 10 families, which are in turn interconnected and form a larger community ($\approx 3 - 4$ co-residing bands or ≈ 30 families) within the metapopulation. For better comparisons with empirical data on social organization, future studies can base their models on empirical ecological or mobility data and investigate the emergence of multi-level sociality in more detail.

These findings hold significant implications for our species' evolutionary history and the ability to develop cumulative culture (Boyd and Richerson, 1995). The degree and strength of intra-and inter-regional group interactions among prehistoric hunter-gatherers and their spatial distribution have been proposed to be key factors for cultural transmission (Romano et al., 2020). The focus of our model was on social network patterns that can arise solely from the derived features of hunter-gatherer foraging-related mobility in different environments, as we wished to unravel their implications for information transmission. Accordingly, we did not consider other social factors that could have shaped their mobility decisions (such as cooperative breeding, resource sharing or joint ritual participation), further structured their interaction networks or potentially resulted in greater incentives and/or efficiency of information transmission. Nonetheless, the model sheds light on the mechanisms by which the regional-scale connectivity generated by individual central-place foraging despite low population sizes throughout our species history. Such connectivity could have maintained cultural diversity and complexity by allowing cultural recombination, transmission of innovations, and preventing the loss of existing culture (Creanza et al., 2017; Dyble, 2018; Hill et al., 2014; Hovers and Belfer-Cohen, 2006; Migliano et al., 2017).

Further research could elaborate on more complex portrayals of physical (for example, resource distribution, traveling costs, seasonality) and social (for example, demography, inter-forager competition, cooperation, sociality, kinship, learning) environments that would have characterized early hunter-gatherer communities. These factors would have potentially interacted with foraging and mobility decisions and cultural complexity (Apicella et al., 2012; Grueter and White, 2014; Shott, 1986; Smaldino and Schank, 2012; Strassberg and Creanza, 2021). Moreover, these factors would have also interacted with the cognitive capacities of our early ancestors (e.g. spatial memory, longer-range planning, larger neocortex, theory of mind, symbolic communication) (**??**). Such cognitive factors would have affected the ability to explore larger spaces, engage in central-place foraging and maintain more extensive social networks, and possibly created selection pressures that paved the way for present-day human cognition and culture (Garg and Kello, 2021; Grove and Dunbar, 2015; Hill et al., 2009; Laland and Seed, 2021; Whiten and Erdal, 2012).

Although additional studies should also address potential selection pressures experienced by our ancestors that would have led them to start using and returning to central places, our study corroborates early claims that central-place foraging would have had important implications for the accumulation and transmission of tools and other types of information (Isaac, 1978). However, our work highlights the role of mobility and spatial patterns that stem from central-place foraging in our evolutionary history. We suggest that mobility-driven networks could have led to positive feedback whereby a more efficient transmission of social and/or ecological information, increased food-sharing, better resource-defenses, and a greater accumulation of material culture at a few places would have been advantageous to central-place foragers (Cartmill et al., 1986; Lehmann et al., 2014). This advantage could have further promoted reliance on increasingly complex culture and encouraged adaptations to social networks (for example, through kinship or trade) to efficiently generate, transmit and sustain such culture (Cantor et al., 2015; Dyble, 2018; Grove, 2018; Hamilton et al., 2007; Smolla and Akçay, 2019; Whallon, 2006).

Chapter 6

Conclusion

Foraging illustrates the general problem of searching for solutions in a problem-space that holds important implications for understanding search heuristics relevant to multiple topics like robotics, reinforcement learning, memory, and decision-making. Further, collective search, where multiple agents interact to collectively work towards finding a solution or accomplishing a common goal, can help us understand how agents can optimally search for solutions together.

Efficient or optimal search behavior is dependent on how individuals or groups balance the various trade-offs associated with search decisions. Through this dissertation, I have presented work spanning from individual-level to group-level foraging and how they can efficiently search for resources under several constraints that pose fundamental trade-offs, between exploring for new information and exploiting previously found information. It further studies how individual and group foraging affect each other and their trade-offs. Below I first summarize the important findings from each study presented here, their significance and broader implications, and then, discuss their overarching contributions and the missing gaps that they highlight.

Study 1

Efficient search for resources with no or limited prior knowledge requires individuals foragers to make a series of decisions regarding how to move to find resources, how much time to spend exploring new areas versus exploiting the areas already accessed, and how much effort to expend in finding resources. We began the dissertation with an experimental study (Chapter 2) (Garg and Kello, 2021) on individual human foragers and how they manage these trade-offs and efficiently search for resources under various constraints. Foraging decisions can be constrained by the properties of their physical environments, for example, resource distribution, and energy landscape. But intrinsic and cognitive constraints such as time, mental effort, prior knowledge, the need to return to a home-base can affect how efficient foragers manage the various trade-offs like exploration vs exploitation, speed vs accuracy of resource detection, or even between movement-based search that costs physical energy but at low mental effort vs perception-based search that can cost more mental effort and planning but preserve energetic reserves.

To test how humans manage these trade-offs to efficiently search in natural environments, we built an ecologically-valid virtual game set in the Himalayas, where players had to find as many resources as possible given a limited energy budget that decreased as they moved across the landscape. They could pause between their movements and carefully scan their surroundings for resources which were often occluded by trees and thus, efficient exploiting required effortful detection. We further created a condition that increased the need for effort and planning by adding a 'home-range' constraint where the players need to return to a home-base to get rewarded for the resources found. We found that irrespective of the home-range constraint, efficient players moved in patterns that closely resembled theoretically optimum Lévy walks with the exponent of 2 and balanced long, exploratory movements with short, exploitative ones.

However, efficient players arranged their Lévy-like displacements into trajectories that were adaptive based on their task condition, with 'home-range' players moving in subdiffusive patterns that confined their search near the home-base, while the 'free-range' players showed quick, super-diffusive patterns that led to extensive exploration of the landscape. Furthermore, this distinction in their movement-based search led to differences in how they expended their time and mental effort in perception-based search and planning their movements. We found that home-range players who were restricted in their overall exploration of the landscape, intensified their exploitative bouts by pausing and perceptually-searching for longer durations than free-range players. By contrast, non-efficient players of the two conditions did not differ much in their search behavior and followed trajectories resembling a random-walk. Taken together, Chapter 2 added important results to the foraging literature that is often divided between optimal foraging theories (Benhamou, 2004) and random-walk based theories (Bartumeus et al., 2005; Viswanathan et al., 1996), and showed that Lévy-like patterns can be generated by non-random, cognitively driven search, and that these basic patterns can be further built upon to adapt to various task constraints and generate behaviors that are not different from OFT predictions. It also highlights the importance of considering the role of mental effort in search decisions (de Froment et al., 2014) and can guide future studies seeking to explore these trade-offs under different task conditions.

Study 2

In the second study (Chapter 3) (Garg et al., 2022), we scaled up from individual-level foraging to group-level. We built an agent-based model to study how groups can efficiently search for resources and how individual-level search behavior affects their performance. When collectively foraging, individual searchers can independently search for resources at potentially higher search costs or use social information to follow a resource patch found by others. In general, groups can benefit from such exchange of information due to reduced search costs but excess information exchange and social learning between individuals can reduce overall levels of exploration and cause groups to get stuck with sub-optimal resource patches or solutions (Clark and Mangel, 1986; Giraldeau et al., 2002; Toyokawa et al., 2019; Webster and Laland, 2012).

However, this balance between group-level exploration and exploitation can depend upon the search strategies of individual foragers and their propensity to socially learn from each other. We found that when in groups, individual foragers should increase their levels of explorative search instead of balancing explorative and exploitative modes that we noted in the last chapter in order to maximize group performance. Furthermore, our results showed that the frequency of social learners in a group can affect the optimal level of social learning individuals should practice. We found that in large groups where the chances of groups being stuck in local minima become more significant, groups can increase their performance when individuals only selectively copy other agents, thus maintaining sufficient exploration levels. We argue that these results hold general implications for any group of multiple interacting individuals that seeks to maximize its efficiency in searching for solutions to a problem and highlight the importance of independent search strategies in studies of collective foraging and problem-solving.

Study 3

While our results showed that the explorative individual strategies are optimal for group search efficiencies, they may not maximize individual-level fitness and be evolutionary stable strategies. In Chapter 4, we extended the collective foraging model to study evolutionary dynamics of different individual search strategies distinguished by their speed of exploration. We found that explorative strategies are generally at a disadvantage and can be invaded by exploitative strategies that can take advantage of the resources found by the former, and result in inefficient groups. Further, rich patches promote higher levels of exploitation in search strategies to increase the time spent near a resource patch than when patches are scarce, which favor faster exit from the resource area due to a high level of competition. However, in conditions of excessive competition such as in large groups, exploitative strategies face lower payoffs and explorative strategies can be evolutionary stable because they allow individuals to separate from other group members, reduce the competition faced, and increase the rate of discovering patches away from others. Furthermore, when agents could efficiently exploit a patch through area-restricted search, explorative strategies have even higher payoffs because they can gain a sufficient share from their findings and then quickly exit to find more patches. Our model adds to the social foraging and producer-scrounger literature and shows that such dynamics can result from the commonly observed variation in animals and humans along the exploration-exploitation axis (Mehlhorn et al., 2015). Further, we show how competition for resources and simple heuristics like ARS can increase payoffs from explorative strategies and increase group efficiencies.

Study 4

In the previous two chapters, we observed the importance of social interactions and movement patterns in modulating group and individual search efficiencies. Movement patterns can affect social interactions and the social networks, too. In the final study (Chapter 5) (Garg et al., 2021), we took a step back and investigated how movements of individual agents driven by foraging decisions can affect social interactions and networks, and subsequently a group's ability to efficiently search and exchange information. We simulated foraging-based movement patterns of hunter-gatherers, a particular case of foragers which represents a significant portion of human evolutionary history (Marlowe, 2005). In general, hunter-gatherers practice central-place foraging where they forage within a home-range and periodically, move the location of their home-bases to maximize their foraging returns (Venkataraman et al., 2017). We found that short-range movements within home-ranges can create strong social communities with frequent and long social interactions, and long-range residential movements can help connect these different communities and result in networks that are efficient at both global and local scales. Our work shows how central-place foraging could have created social networks that were efficient at information-exchange, cultural transmission, and collective search efficiency. It adds an important dimension to the literature on hunter-gatherer networks and highlights how movement and foraging decisions could have played in our ancestors' social networks.

Final remarks

Taken together, the work presented here examined the trade-offs that arise in individual and collective foraging, and how they can be managed under different physical and social environments. Our work demonstrates that explore-exploit (EE) trade-offs can manifest in different forms, and interact across scales. We show that efficient individual-level foraging needs to balance global exploration of a landscape and local exploitation of the areas found, and that this balance shifts based on the task and cognitive constraints. We further highlight how EE behaviors can frame other trade-offs like speed vs accuracy, physical search vs mental effort, and how Lévy-like search patterns can balance these trade-offs.

However, at the level of collective foraging, we found that efficient foragers need to balance a different trade-off between independently searching and using social information, in addition to managing EE in their independent search strategies. We found that in groups where exploiting social information is useful, individuals should balance social learning with explorative independent search. Furthermore, we show how these individual-level decisions can affect group-level EE balance: excessive social learning by individuals can reduce the group-level exploration and diminish group performance. Our evolutionary model further investigated the evolution of explorative and exploitative search strategies in groups and showed that competition for resources can lead to groups composed of explorers and exploiters. It also shed light on how heuristics like area-restricted search that help explorers to effectively exploit resource patches can promote the evolution of explorative strategies and increase collective gains. Finally, we looked at the effect of exploitative and explorative foraging movements in hunter-gatherers on the structure of their social network and its abilities to balance exploitation and exploration of cultural knowledge. This work thus demonstrates how EE trade-offs can interact across scales and give rise to adaptive behavior.

Although the studies presented in this thesis thoroughly investigated the topics at hand, certain general caveats remain to be addressed. The general theme of the work here is based on the principle of optimality, which considers intelligent human and animal behavior as optimizing various costs and benefits associated with it. While this principle aids tractable modeling, it may not represent actual, real-world behavior. Many theories suggest the presence of ‘rules of thumb’ or simple heuristics that are favoured by natural selection and can help a forager approximate optimal strategies without the need of ”calculating the exact solutions” (Krebs et al., 1983). Animals and humans may practise satisficing heuristics that are not optimal but economical to achieve *fast and frugal* solutions (Gigerenzer, 2011; Gigerenzer and Sturm, 2012; Simon, 1956). In terms of the work presented here, it is possible that actual human and animal behavior does not closely follow optimal patterns and rather adopts simpler approximations of the optimal behaviors. Our work on the costs of mental effort suggests a possible bridge between optimality and satisficing theories: by including costs of mental effort such as planning, cognitive processing, and attention, optimality theories may be able to more closely approximate real-world behavior.

Satisficing behaviors might be prevalent in groups, too. Our results from collective foraging also suggest that groups may not always evolve to maximize their performance, especially when less optimal strategies have similar payoffs as the optimal ones. For instance, innovations should generally always increase the performance of social groups by finding new solutions. However, innovations can be costly and risky, while social learning can provide reasonably good solutions at lower costs. In addition, certain social learning strategies such as conformist learning may be generally adaptive but not across all contexts and may cause individuals to learn irrelevant or even maladaptive behaviors, for example, the spread of fake news or panic rushes in crowds(Kendal et al., 2018; McGuigan, 2012). Nevertheless, such strategies might be maintained in population despite their adverse effects. For example, some studies have shown that nonhuman primates sometimes copy only instrumental behaviors, but humans tend to copy both relevant and irrelevant behaviors (Horner and Whiten, 2005; Jagiello et al., 2022), which might form the bedrock of our highly adaptive cultural abilities.

The other major caveat of these studies is that they focus on pattern-level behavior and largely ignore the underlying mechanisms. The thesis cements the optimality of Lévy-like patterns in general search processes, but the mechanisms that can generate such patterns need further investigation. We mention a few putative mechanisms, such as trade-offs between exploration and exploitation, speed and accuracy, and optimal foraging behavior. However, while they provide a way to model foraging decisions, they do not provide details on the mechanisms that underlie them. Similarly, the role of individual learning and cognition in the efficient exchange of information and social learning needs to be given more attention. For example, a better understanding of the goals of other members, a better ability to estimate payoffs from an option would lead to more efficient social learning, information exchange, and even communication (Heyes, 2016; Laland et al., 2011), and in turn, affect the optimal social learning strategies.

Finally, the studies presented here consider behavior at different levels, from individuals to groups and networks, and to an extent, considers the interplay between them. However, the interplay between these levels has been so far understudied. For instance, optimal foraging and Lévy walk theories have primarily focused on individual-level behavior, but, as the thesis suggests, the predictions from these theories change when we consider group-level behavior. Thus, it is essential to extend these theories to incorporate social contexts. Further, the interplay between individual-level behavior on social networks and structures has been largely overlooked, too. For example, variation between individuals in their exploratory behavior might affect the positions they acquire in social networks and determine how information is exchanged across the networks. Conversely, social environment, or the immediate social neighborhood of an individual may affect the strategies it adopts.

In conclusion, the dissertation began with a study on individual foraging and the various trade-offs of exploration and exploitation, speed and accuracy that an individual forager faces. It then scaled up to group foraging and looked at how individuals in groups face modified trade-offs and how their search strategies affect group efficiency. In addition, it looked at the evolution of explorative and exploitative search strategies in groups and its implications for group behavior. Finally, it also considered the effect of individual foraging and movement decisions on social networks and their consequences on human cultural and social evolution. Going forward, future studies can build upon the work presented here and address their gaps towards a clearer picture of foraging and search processes, and adaptive behavior at multiple levels of organization.

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Appendix A

Appendix for Chapter 3

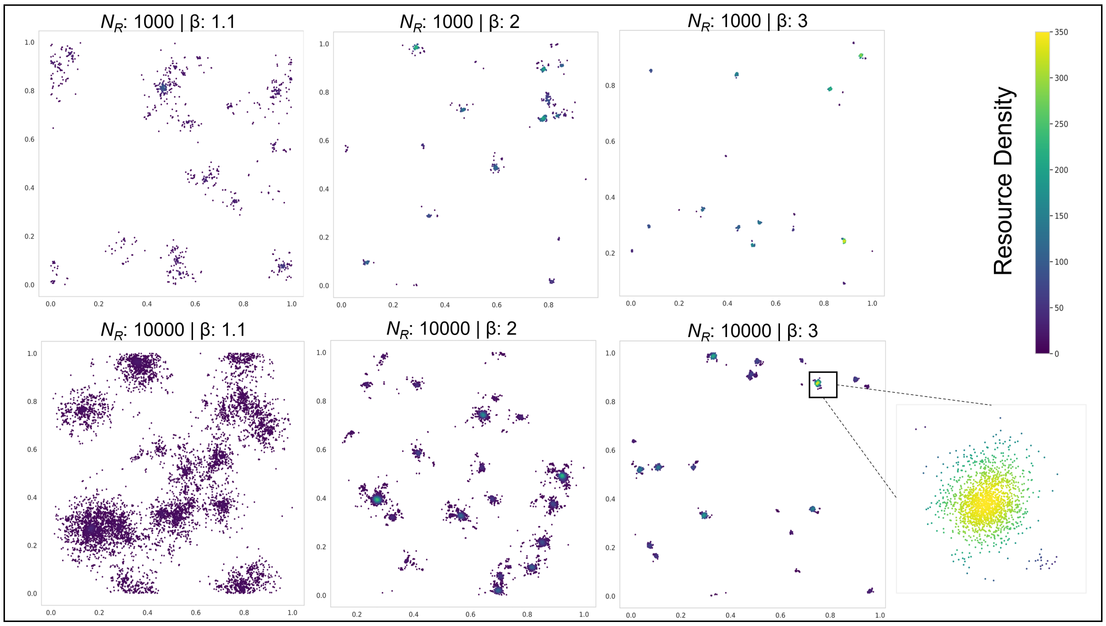

Figure A.1: Examples of the resource distributions generated by the power-law growth algorithm. The color-map indicates the density estimates (calculated using Gaussian Kernel Density Estimation) of resources present at a location. Clockwise: $N_R = 1000, \beta = 1.1$; $N_R = 1000, \beta = 2$; $N_R =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

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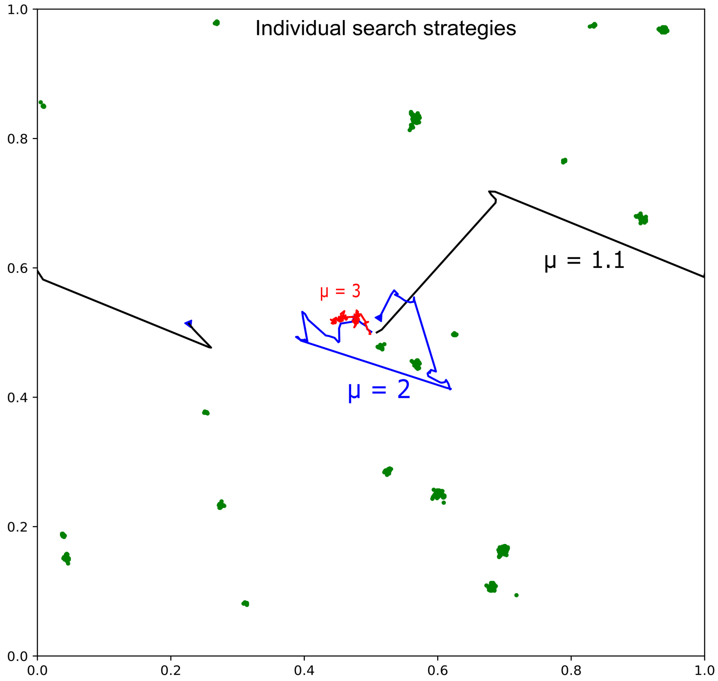

Figure A.2: The different individual search strategies used in the model after 1000 time-steps.

A.1 Methods

Trajectory Analysis

We defined a step as a continuous straight-line movement which could be truncated by finding a resource, finding another agent, or completing a random walk. For every run, we calculated the observed Lévy exponent (μ') for every individual trajectory and took their average to estimate the lévy exponent at the group-level (see Figs. A.7a and A.7b for examples of the path distributions). We used the *powerlaw* package in Python to fit the trajectories to truncated power-laws alstott2014powerlaw.

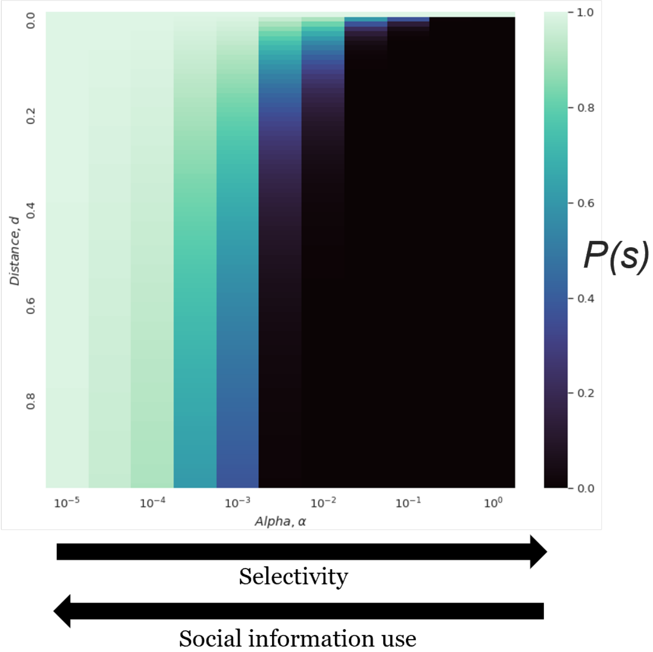

Figure A.3: The effect of α and distance from another agent on the probability to use social information ($P(s)$).

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Cluster Analysis

We used DBSCAN (Density-based spatial clustering of applications with noise) to detect sub-groups/clusters of agents at every time-step during the simulation. A cluster was defined as a group of minimum of 3 agents with a maximum distance threshold (d) of 0.1. If a cluster detected at time, t was also detected at t + 1, we counted that as a single cluster, added a unit to the duration of the cluster, and updated the number of agents in it. A new cluster at time, t was defined if its centroid was not within d of any of the clusters detected at the previous time-step, t - 1.

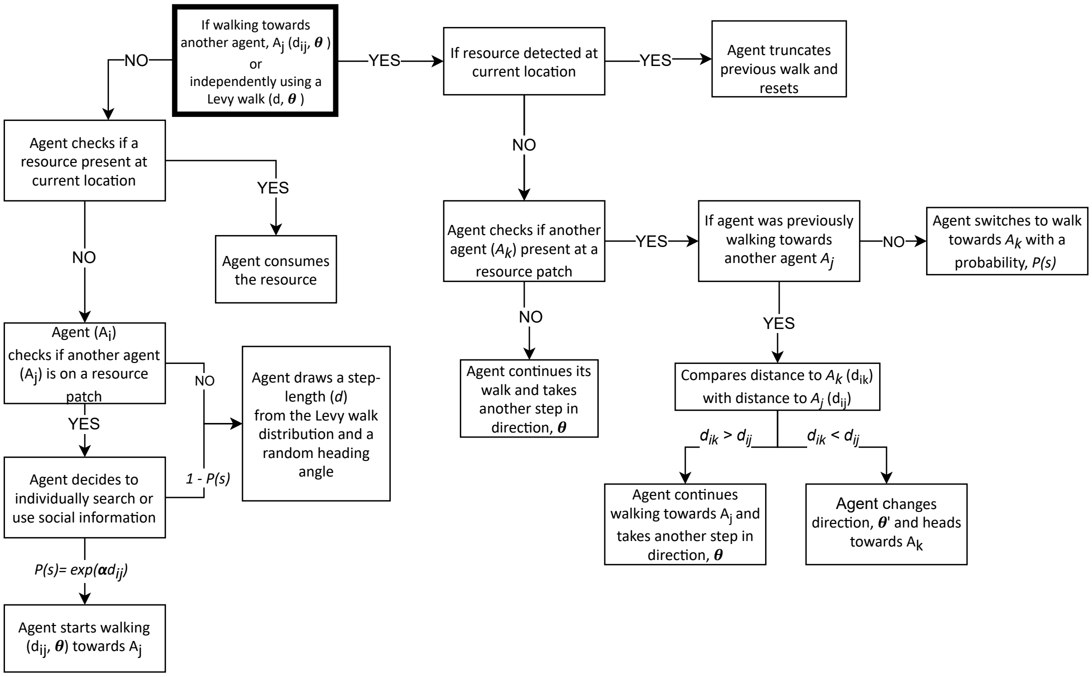


Figure A.4: A flowchart describing the rules that agents followed in the model.

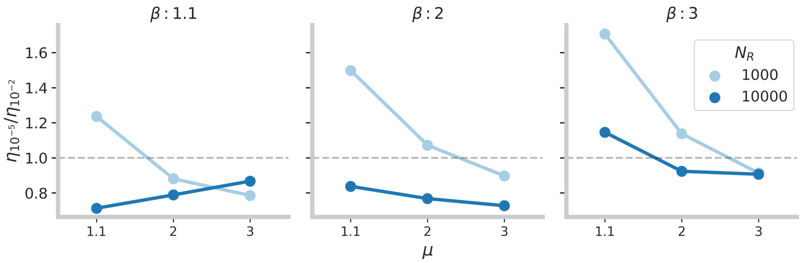


Figure A.5: The advantage of minimally-selective social learning ($\alpha = 10^{-5}$) relative to more selective social learning ($\alpha = 10^{-2}$) for different Lévy walks and in different resource environments. Dashed line indicates when the two levels of social learning selectivity are equivalent.

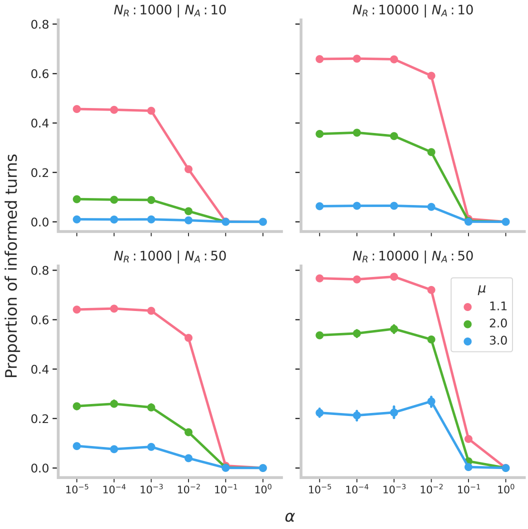


Figure A.6: Proportion of informed turns taken by agents, for $\beta = 3$. Error bars indicate 95% confidence intervals.

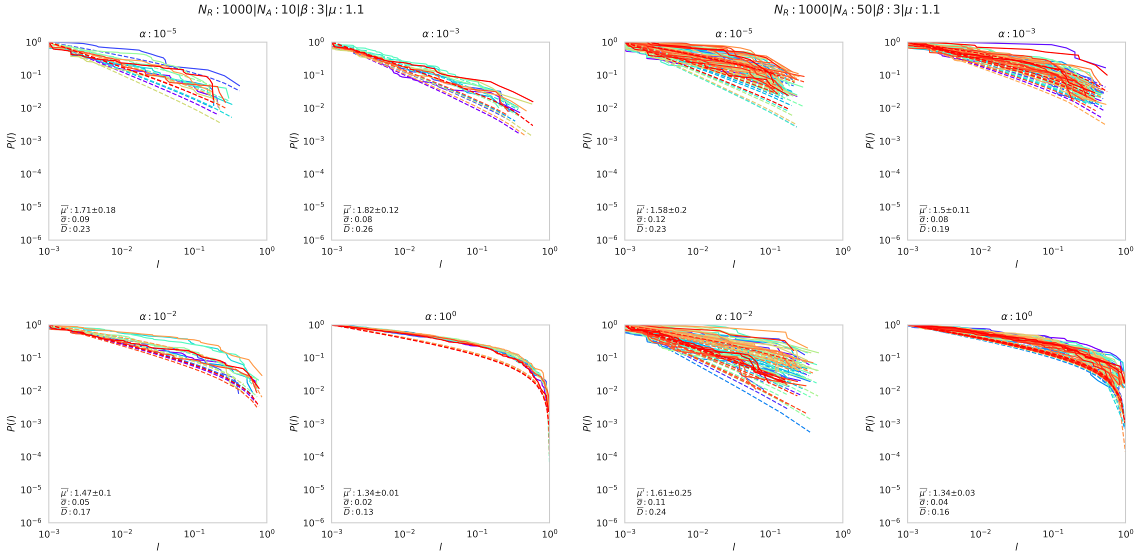
A.2 Results

Lévy distribution plots

Our results show that under most conditions, the observed Lévy exponents remain similar across agents within a given run (Figs. A.7a, A.7b). A larger group size increases the variability within the population because not every agent explores or exploits equally. Similarly, an intermediate value of $\alpha \approx 10^{-2}$ increases variability between group-members because not every agent is likely to either produce or scrounge which alters their movement patterns.

Population-level variability and correlations between observed Lévy exponents and search efficiencies

When the original search strategy was explorative with $\mu = 1.1$, agents increased their efficiency by adding short steps to their trajectories that helped them exploit resources and caused $\mu' \to 2$ (Fig. A.8(a)). However, when resources were rich ($N_R = 10000$) and agents needed to engage in exploitative search more, higher search efficiencies corresponded with $\mu' \to 3$ (Fig. A.8(b)). Furthermore, in conditions with



(a) $N_A = 10$

(b) $N_A = 50$

Figure A.7: Example of CCDF plots of displacements (l) from individual agents' trajectories in a simulation. Different colors show the probability distribution for individual agents. Dashed lines depict the theoretical power-law fit. $\overline{\mu'}$, $\overline{\sigma}$, $\overline{D}$ represents the mean observed Lévy exponent ± standard deviation, mean MLE error estimate, mean Kolmogorov-Smirnov distance of all agents in the simulation, respectively.

dense clusters and large groups ($N_A = 50$) (Fig. A.8(d)), agents with $\mu' > 3$ were more efficient than agents with $\mu' \leftarrow 2$ because it was advantageous to invest in exploiting rich resource clusters than explore the environment with long steps.

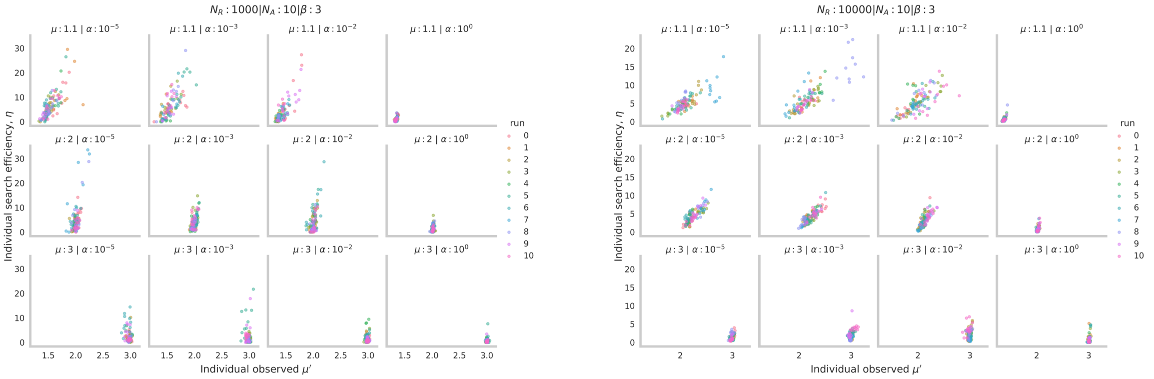
These plots also show the population-level variability in search efficiencies and μ'. We can see that agents within a population varied more when groups were large ($N_A = 50$) (Fig. A.8(d)). Since we stopped the simulation when a group finished 30% of resources, our simulations did not ensure that every agent consumed the same amount of resources. This variability was further exaggerated in large groups because there was higher competition for resources between agents and consumption of resources by a few agents could quickly end simulations. In addition, we can see higher variability in μ' and search efficiency when social learning strategy was selective ($\alpha = 10^{-2}$) than when they were minimally-selective ($\alpha = 10^{-5}$) or only searched independently ($\alpha = 10^{0}$). The inherent variability in selectively using social information can explain this effect.

Temporal analyses

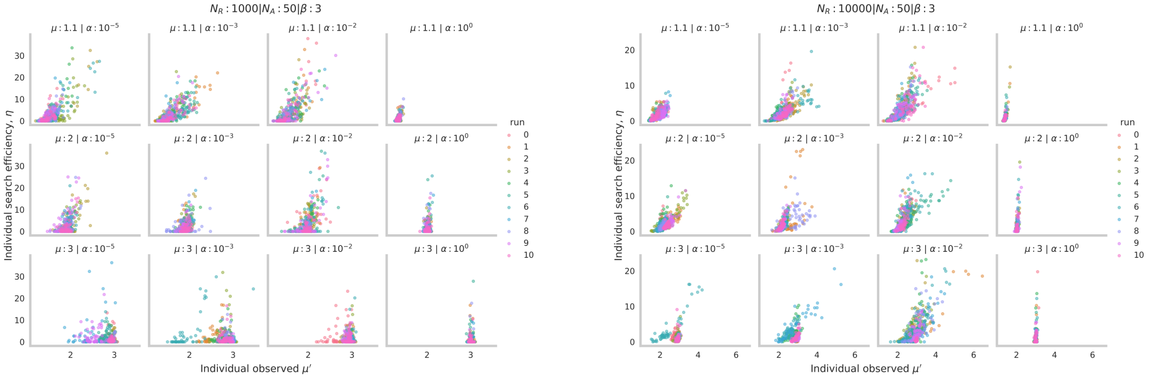
To understand how resources deplete during the course of simulations and how that affects group performance and agent movements, we plotted percent of resources depleted, mean search efficiency and observed Lévy exponent (μ') as a function of time (Figs A.9, A.10). The amount of resources depleted and cumulative mean search efficiency were calculated at every time-step and every 50 time-steps, respectively. We calculated μ' by analyzing path-length distributions within bins of 200 time-steps. In other words, μ' value for time, t represents agents' movement patterns only between the period of $t - 200$ and t.

Our results indicate that in highly clustered environments, resources depleted in a saltatory fashion, where once a resource cluster was discovered, agents engaged in exploitative search that increased their μ', and increased their search efficiency. On the other hand, when a resource cluster was depleted, agents' shifted back to exploratory search that decreased their μ' and search efficiency. However, these patterns were affected by group size (N_A), resource density (N_R), and social learning strategy (α).

For instance, when resource density ($N_R = 1000$) and the amount of social learning



(a) $N_A = 10$; $N_R = 1000$ (b) $N_A = 10$; $N_R = 10000$



(c) $N_A = 50$; $N_R = 1000$ (d) $N_A = 50$; $N_R = 10000$

Figure A.8: Correlation between individual search efficiency (y-axis) and observed Lévy exponent (μ') in different simulations for $\beta = 3$ and different values of α and μ. Different colors are used to distinguish between different runs/simulations

low ($N_A = 10$, $\alpha = 10^{-2}$), resource clusters were not exploited instantaneously in the beginning of the simulation (see Fig. A.9b). In contrast, for $\alpha = 10^{-5}$, agents readily exploited social information and resources depleted faster right from the beginning of the simulation (Fig. A.9a). Furthermore, the saltatory pattern or alternating periods of exploration and exploitation were more pronounced in rich clusters ($N_R = 10,000$) than in less dense clusters ($N_R = 1000$) because agents had to spent more time exploiting resource clusters when they were dense and rich.

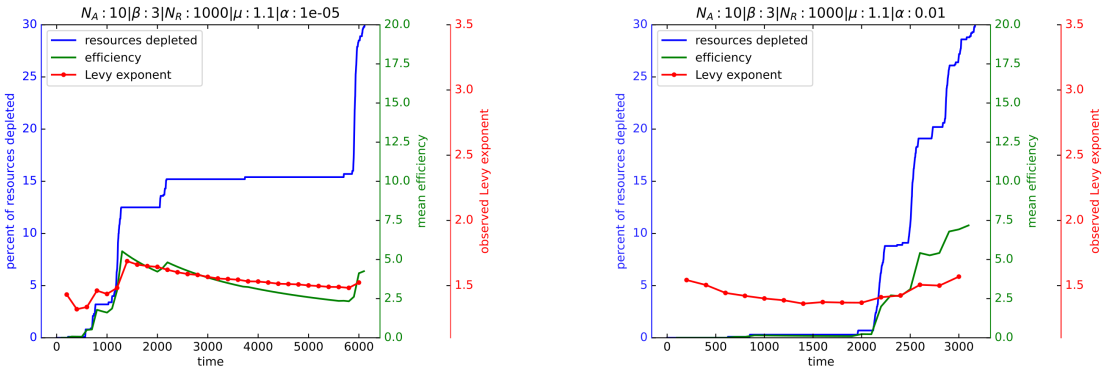
The temporal dynamics also show the effect of excessive social learning in large groups ($N_A = 50$) and dense resource clusters ($N_R = 10,000$). In these conditions, our results (see main text, section 3.4) show that minimally-selective social learning ($\alpha = 10^{-5}$) is less efficient than a selective strategy ($\alpha = 10^{-2}$) because the former causes agents to excessively converge onto one or two resource clusters while leaving others unexplored. In the plots of temporal dynamics (Fig. A.10c), we can see that when resources depleted initially (between 0-1000 time-steps), the Lévy exponent increased rapidly as agents converged to a cluster. This increase was then followed by a shift to explorative search and slower resource depletion. On the other hand, when agents were selective in their social learning strategy (Fig. A.10d), resources depleted steadily and continuously, and agents exhibited a more exploitative search because they simultaneously exploited multiple resource clusters which decreased competition and allowed them to exploit clusters for a longer time.

subsectionProducer-scrounger

We found that when individuals were exploratory, small groups (N_A) could afford to be composed of purely scroungers (Fig. A.11a). But as individual exploration decreased, the optimal composition involved a mix of producers and scroungers (with $\mu \to 3$ or large group sizes). We also found that in cases when more social learners were present ($N_A = 50$; $\beta = 3$) (Fig. A.11b), the search efficiency of a group with a mix of producer-scroungers ($\eta \approx 2$) was lower than a group composed of selective social learners ($\eta_{10^{-2}} \approx 3$).

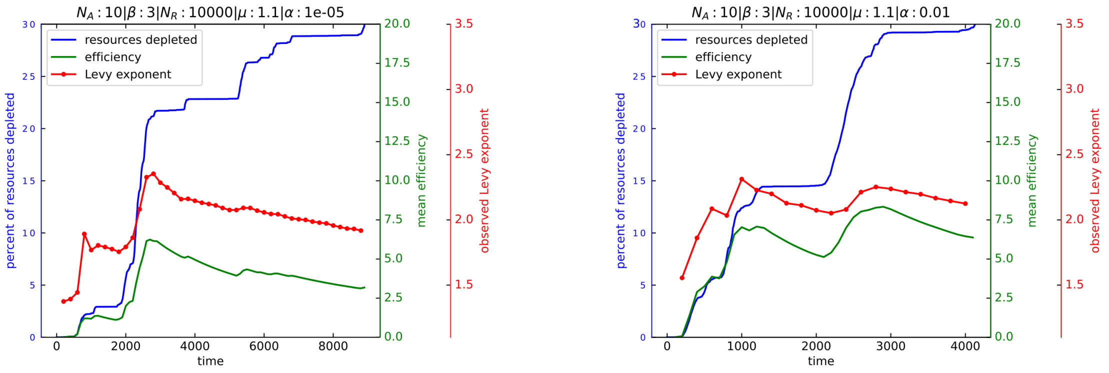
Cluster analysis

We found that subgroup sizes and their duration increased with an increase in group size and resource abundance. Subgroup size was inversely proportional to how selective agents were in using social information, with largest subgroups for minimally-selective social learning ($\alpha = 10^{-5}$). When compared to the most efficient strategies, we can see that the optimal subgroup size was $\approx 5 - 6$ agents in the model. The duration was substantially affected by the individual search strategy given by μ, where $\mu = 3$ caused convergence between agents for the longest durations. However, this effect was more significant when the group size was smaller ($N_A = 10$) because the agents spent more time exploiting a resource cluster than when there were more agents present.



(a) Minimally-selective social learning

(b) Selective social learning

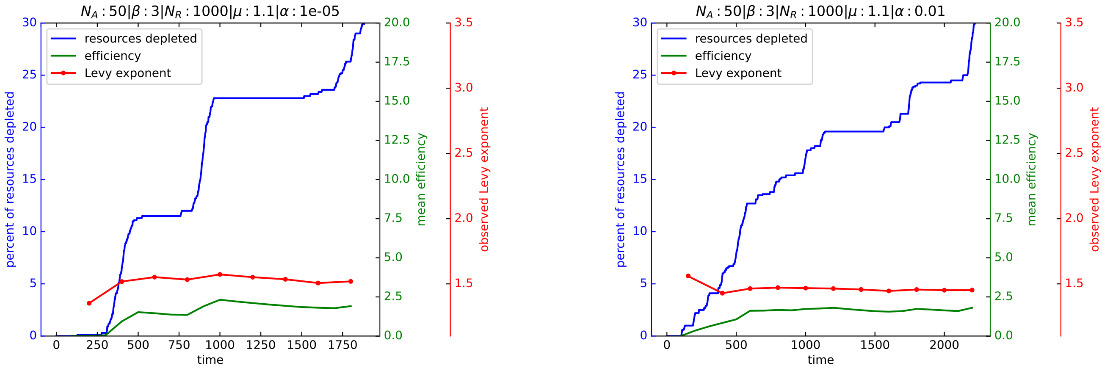


(c) Minimally-selective social learning

(d) Selective social learning

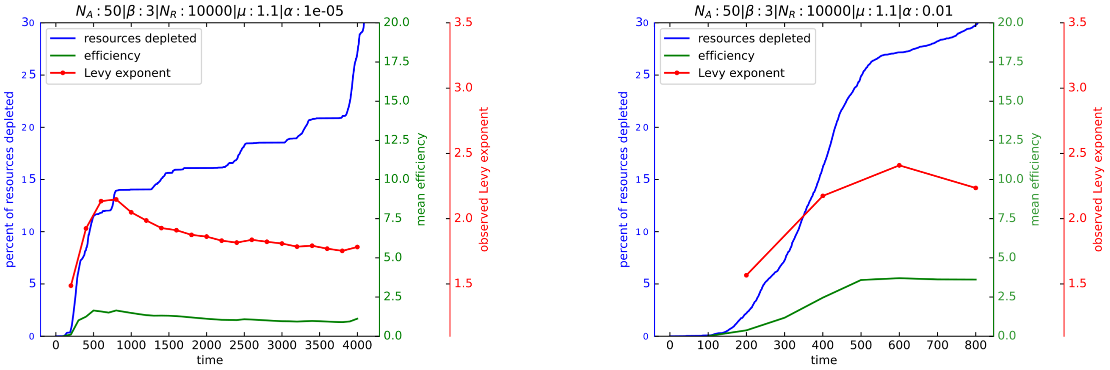
Figure A.9: Example of temporal dynamics of resource depletion (blue), mean search efficiency (green) and observed Lévy exponent (μ') (red) from one simulation/run for $\beta = 3$, $N_A = 10$.

We also looked at how many sub-groups were formed simultaneously under different conditions. We found that when group size was large ($N_A = 50$), less selective social learning ($\alpha \to 0$) created larger (8-10 agents) and fewer(2-3) sub-groups than selective social learning ($\alpha = 10^{-2}$). Selective social learning created smaller (6-8 agents) and multiple (3-4) sub-groups. We would like to note that although the plot shows largest number of sub-groups formed even when there was no social learning ($\alpha \to 1$), this effect is merely an artifact of larger group sizes. When groups were large, the probability of multiple agents being close to each other was higher than



(a) Minimally-selective social learning

(b) Selective social learning

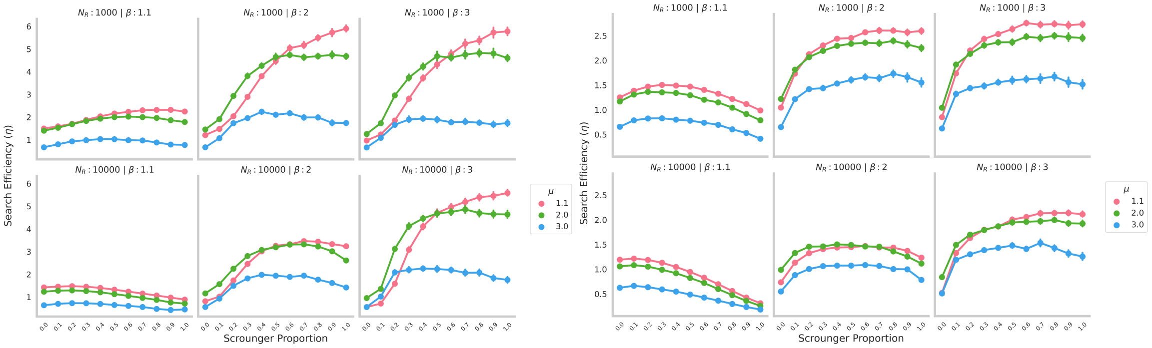


(c) Minimally-selective social learning

(d) Selective social learning

Figure A.10: Example of temporal dynamics of resource depletion (blue), mean search efficiency (green) and observed Lévy exponent (μ') from one simulation/run for $\beta = 3$, $N_A = 50$.

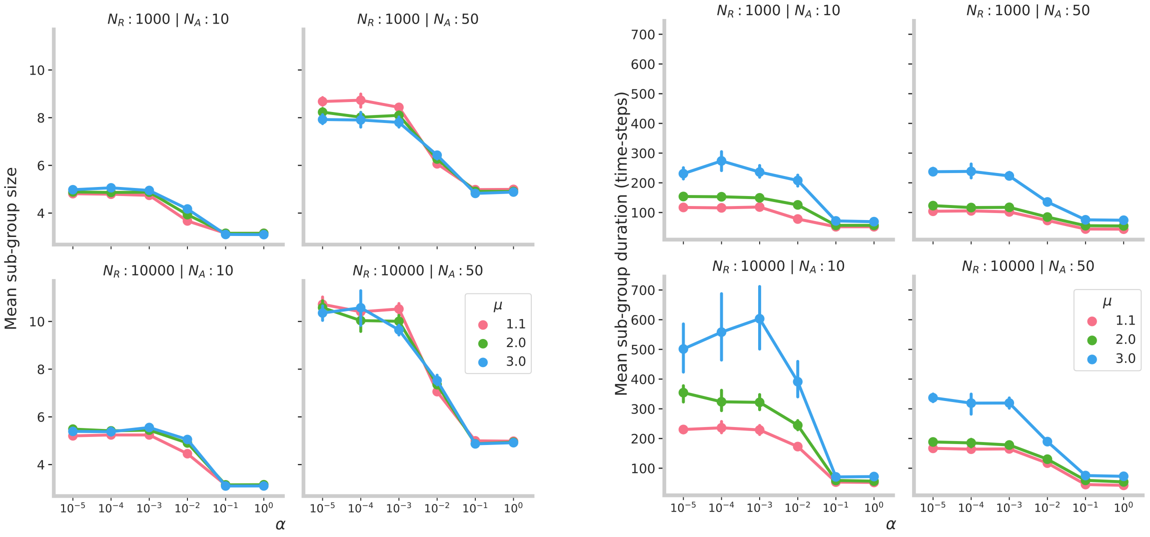
when group were small.



(a) $N_A = 10$

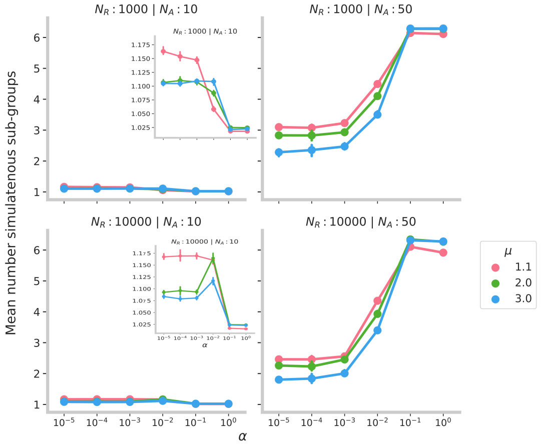
(b) $N_A = 50$

Figure A.11: Performance of groups with different producer-scrounger proportions.

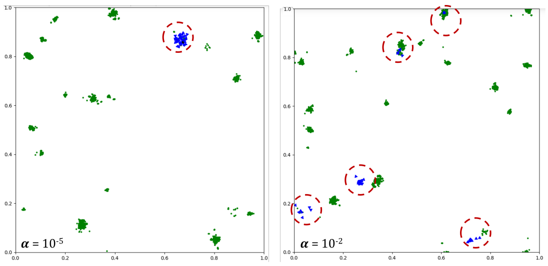


(a) Mean size of clusters/sub-groups

(b) Mean duration of clusters/sub-groups



(c) Mean number of simultaneous clusters/sub-groups



(d) Screenshot

Figure A.12: **(a-c)** Mean size, duration and simultaneous number of clusters/subgroups of agents that formed during simulations, for $\beta = 3$. **(d)**Sub-grouping in groups of size 50 ($\beta = 3; N_r = 10000$). *Left:* When agents use a minimally-selective strategy, they eventually coalesce into a large group of agents. *Right:* A more selective use of social information allows agents to form multiple sub-groups of agents that increase the group's efficiency. Agents are depicted in blue and resources in green.

Appendix B

Appendix for Chapter 4

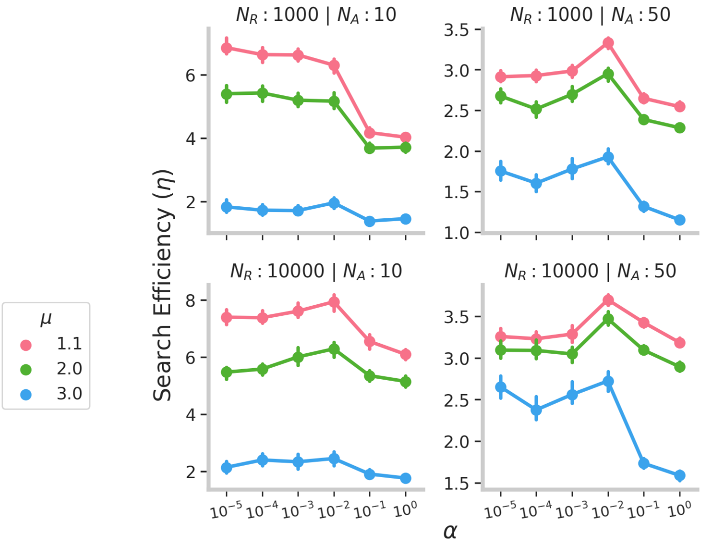


Figure B.1: Group search efficiency η for the ARS model as a function of social selectivity parameter α, Lévy exponent μ, resource density N_R. Error bars indicate 95% confidence intervals.

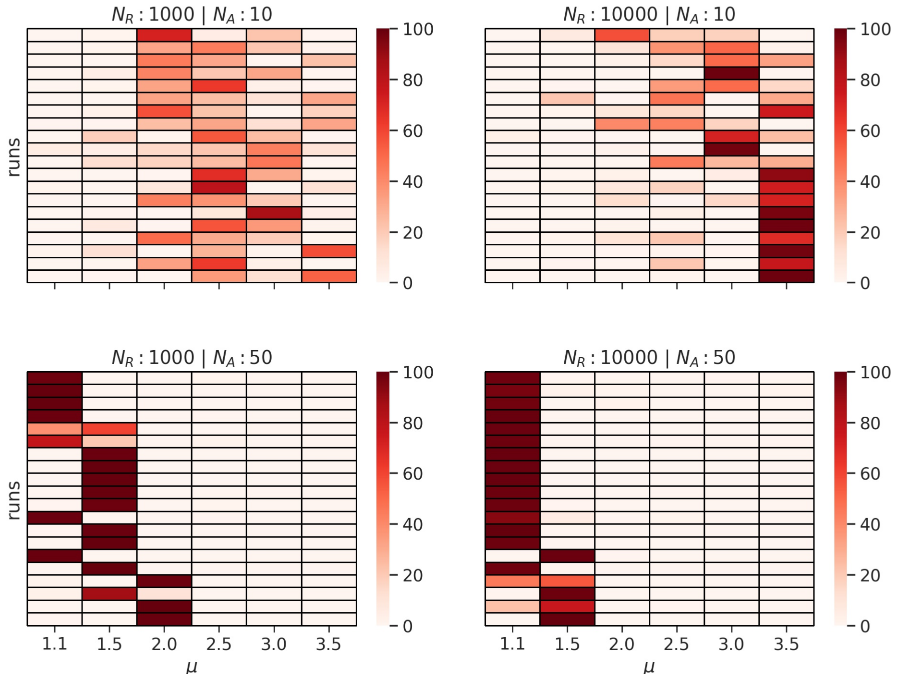


Figure B.2: Mean percentages of different search strategies (columns) over the last 1000 generations for 10 runs (rows) and for $\alpha = 10^{-5}$

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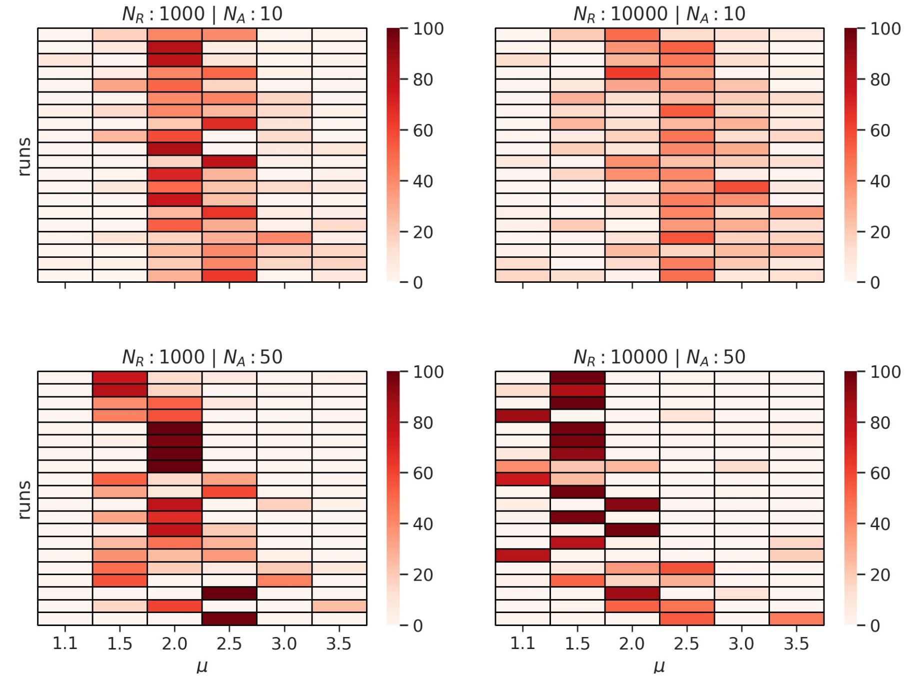

Figure B.3: Mean percentages of different search strategies (columns) over the last 1000 generations for 10 runs (rows) and for $\alpha = 10^{-2}$

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Appendix C

Appendix for Chapter 5

C.1 Methods

In the original formulation, weights represent distance, meaning information travels more slowly along heavier edges. In our models, weights represent social proximity and, therefore, we use their inverse when calculating efficiency. The underlying logic is the same: networks where all nodes are close to one another are more efficient than those where larger distances must be traveled before connecting any two given vertices.

Global efficiency:

Let N be all sets of nodes in the network, n the number of nodes in the network, and w the edge weights.

$$E^w = \frac{1}{n} \sum_{i \in N} \frac{\sum_{j \in N, j \neq i} (d_{ij}^w)^{-1}}{n-1}$$

Local efficiency:

Let nodes i and j be connected through edges with weight w_{ij}, let k_i be the degree of node i, and let $d_{jh}(N_i)$ be the length of the shortest path between j and h, including only i's direct ties.

$$E^{w}_{loc} = \frac{1}{n}\sum_{i\in N}\frac{\sum_{j,h\in N, j\neq i}(w_{ij}w_{ih}[d^{w}_{jh}(N_i)]^{-1})^{\frac{1}{3}}}{k_i(k_i-1)}$$

The original formulation of shortest distance calculations consider weights as distance (e.g. an edge of weight (w_{ij}) 4 between two nodes(i, j) will be considered to have a longer distance, $d_{ij} = 4$ than another edge with lower weight, $w_{ik} = 1$). In our model, weights represent social proximity, and larger weights should decrease path length and speed up information transmission. To correctly represent this, we take the inverse of edge weights and add a unit to the inverses (e.g., d_{ij} would change to $\frac{1}{4} + 1 = 1.25$, and $d_{ik} = 2$), such that each edge has a weight 1 and the maximum efficiency of an unweighted equivalent network is 1. It is important to note that we only use this transformation when calculating efficiencies. The contagion simulations below use the weights as the simulations produce them without any transformations.

Louvain community detection:

Louvain detection method is a hierarchical clustering algorithm, that recursively merges communities into a single node to find clusters with high modularity. It compares the density of connections within a community to the density of connections expected from a random network.

C.2 Results

Resource depletion To better describe the workings of the model, we calculated a metric to show how the resources deplete within an environment for different foraging strategies. First of all, the environments not only vary in their heterogeneity but also in their total resource content. Environments with lower beta values are more abundant overall (see $\beta = 1.5$) than the environments with higher beta values (see $\beta = 4.5$). Secondly, when the environment is abundant ($\beta = 1.5$), foragers do not move or coincide much causing the patches to deplete in a linear fashion. However, when the environment is heterogeneous and some patches are richer than others ($\beta > 1.5$), foragers coincide at those rich patches more frequently and the patches deplete in a non-linear fashion. These patterns are congruent with realistic trends, whereby resource clustering leads to agents coinciding in the same patches and thus making them deplete disproportionately faster than the surrounding ones. We also found that the foraging strategy with different radii also effects the rate of resource depletion. When the radius is large ($r = 1$), foragers are not constrained within their foraging/logistical radius and can move longer distances to consume rich patches, the resources deplete at very fast rate. But when the radius is smaller, the patches deplete at a lower rate.

Sensitivity analyses

To check the robustness of our results, we ran the simulation for 1000 time-steps and calculated network metrics (number of total interactions, number of unique interactions, number of components, local and global efficiency) every 100 time-step. We found that our results were consistent regardless of the number of time-steps that the models ran, and the networks created by central-place foragers with intermediate radius in heterogeneous environments were both globally and locally efficient.

We found that in most of the environments, the efficiency parameters plateaued after certain time-steps. In environments with intermediate to low heterogeneity ($\beta \geq 2.5$), the number of interactions between foragers grew quickly at first and then decayed as foragers depleted the resources. As resources depleted, patches could no longer sustain large numbers of foragers, and the local efficiency remained relatively constant after 100-time steps (Fig. C.1).

However, we found that the global efficiency continued to grow for a longer duration, especially in $\beta = 2.5$ (Fig. C.7). As the foragers continued to move across the landscape and interacting with previously unconnected foragers (see number of unique interactions in Figs. C.9, C.8), the number of sub-groups/components decreased (Fig. C.6) and the network grew in size that made the networks more globally efficient. When the environment was abundant with many rich patches ($\beta = 1.5$) and the rate of patch depletion was low, foragers moved less frequently and continued interacting with previously connected foragers (with negligible unique interactions across 1000 time-steps). This caused local efficiency to continue growing over the 1000 time-steps but global efficiency stayed constant at a minimal value.

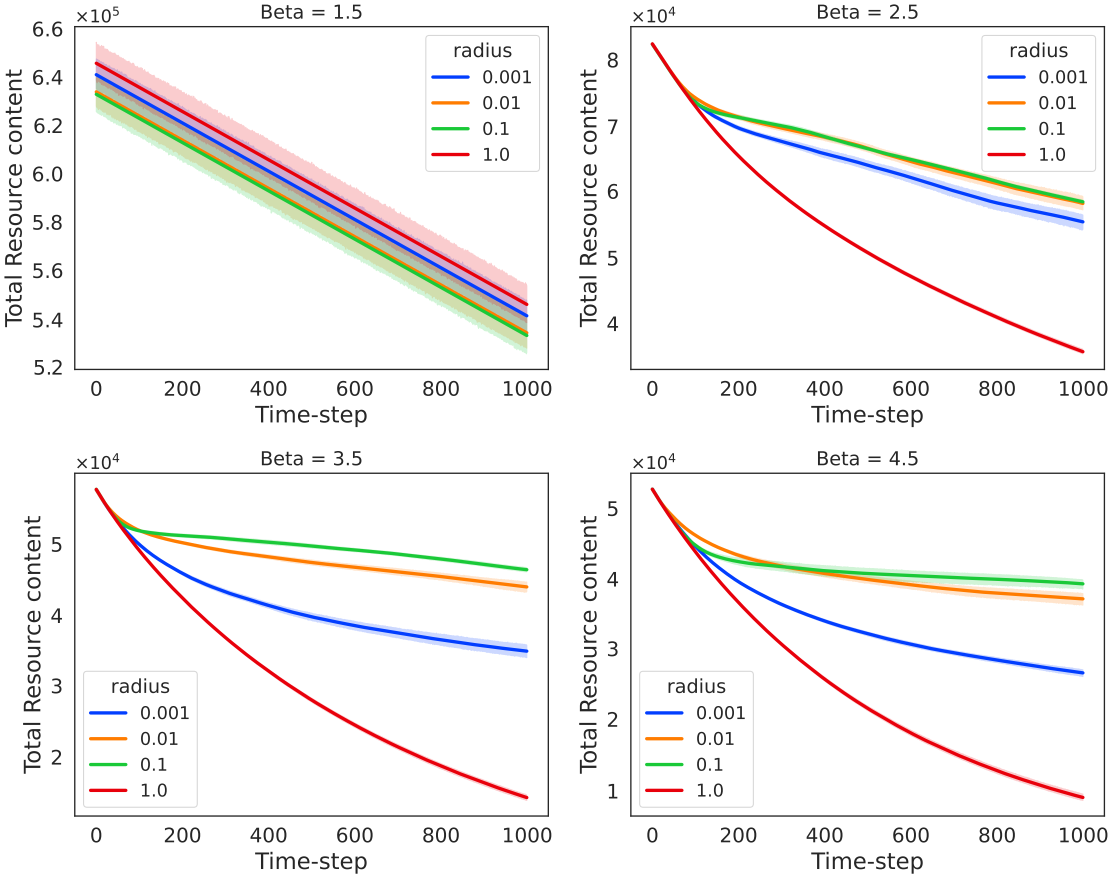

Figure C.1: Resource depletion in the model environment with 100 foragers over 1000 time-steps.

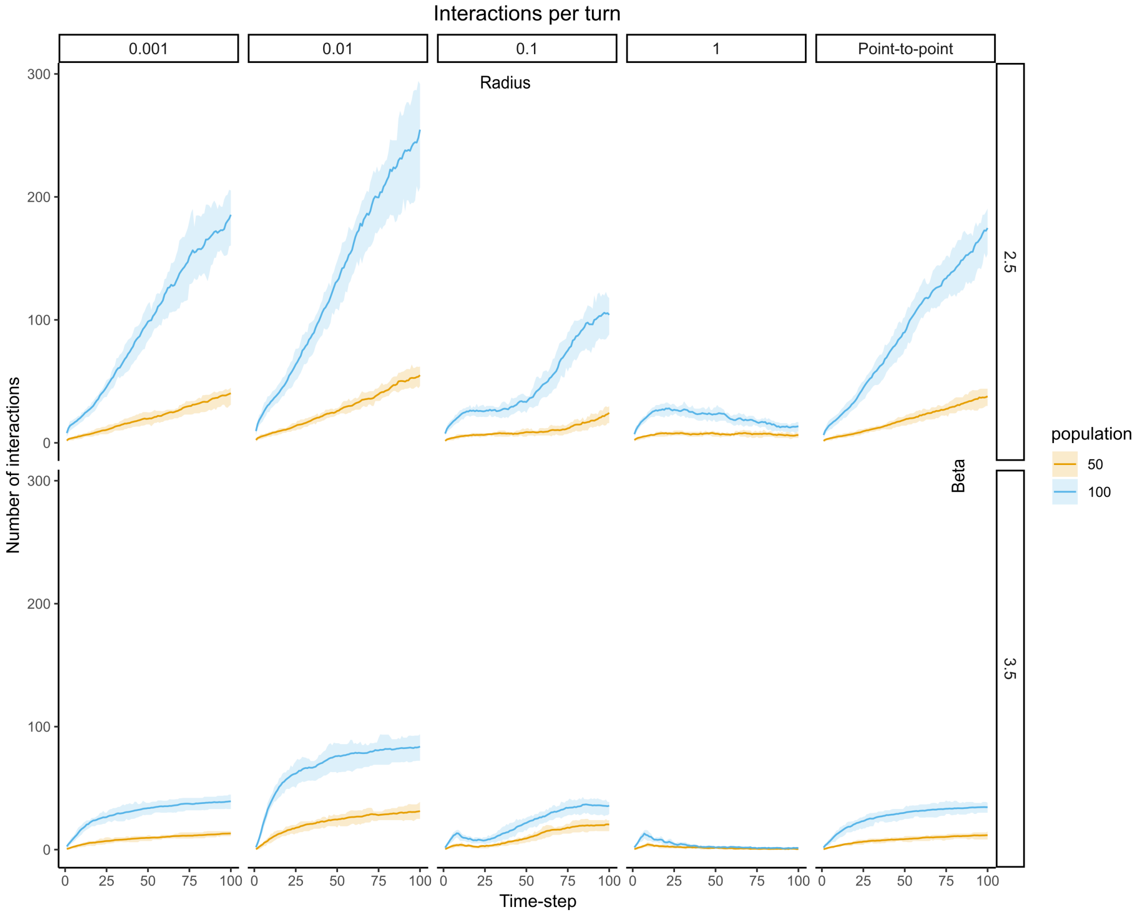

Figure C.2: Interaction per turn for all parameter combinations.

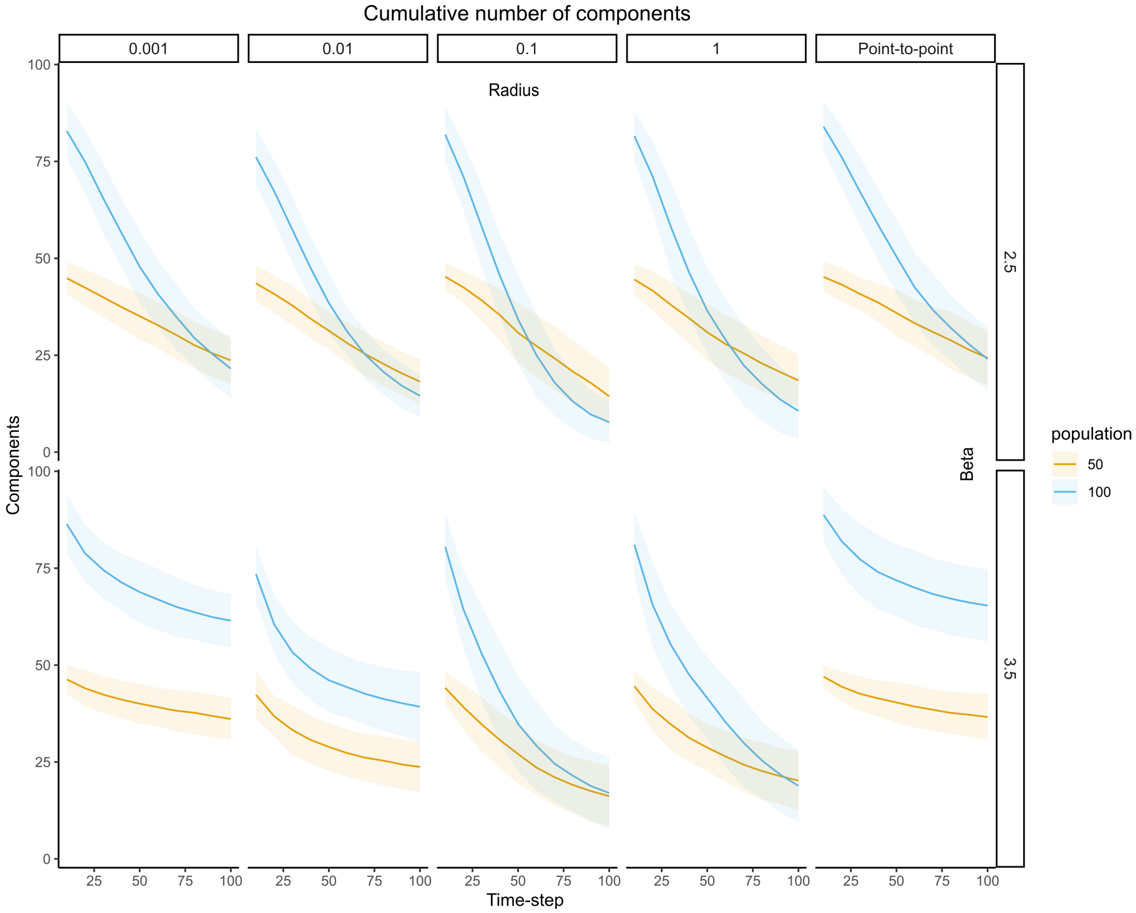

Figure C.3: Components per turn for all parameter combinations.

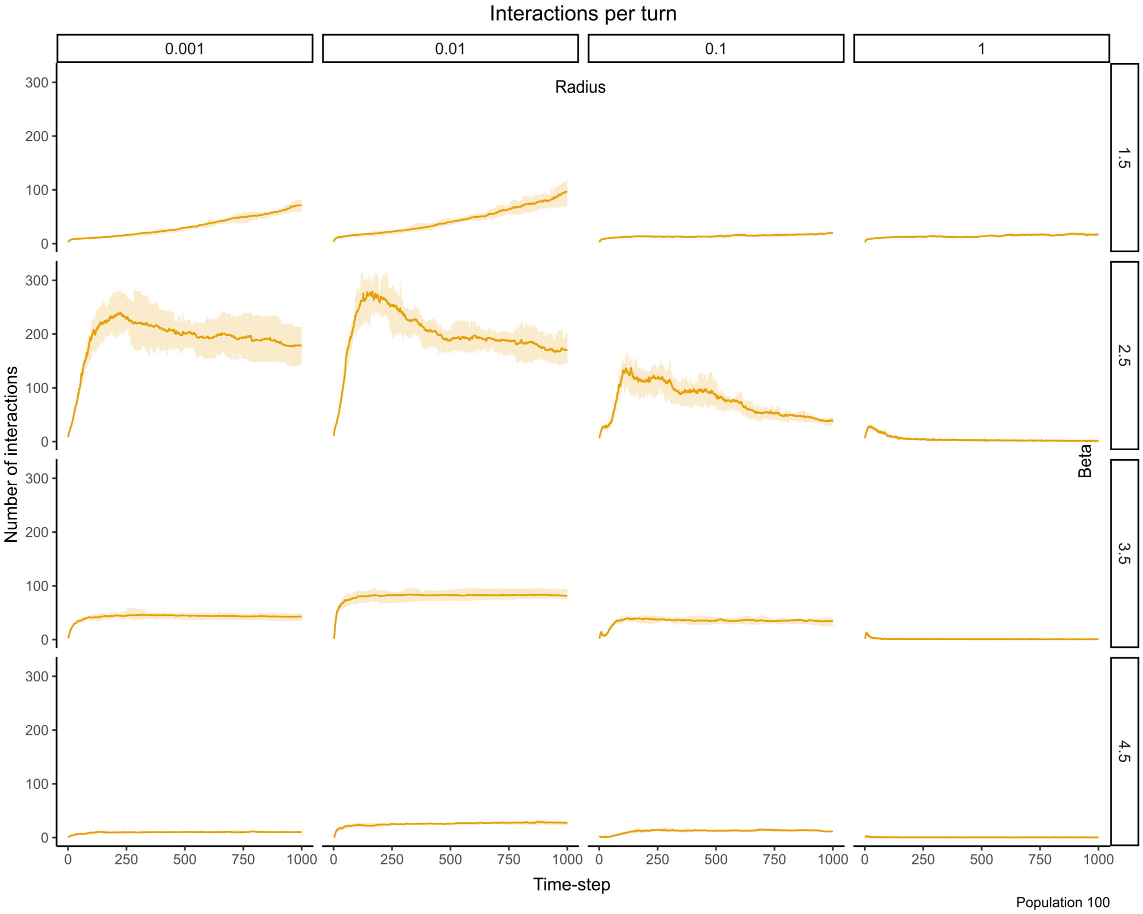

Figure C.4: Interactions per turn for 1000 time-steps.

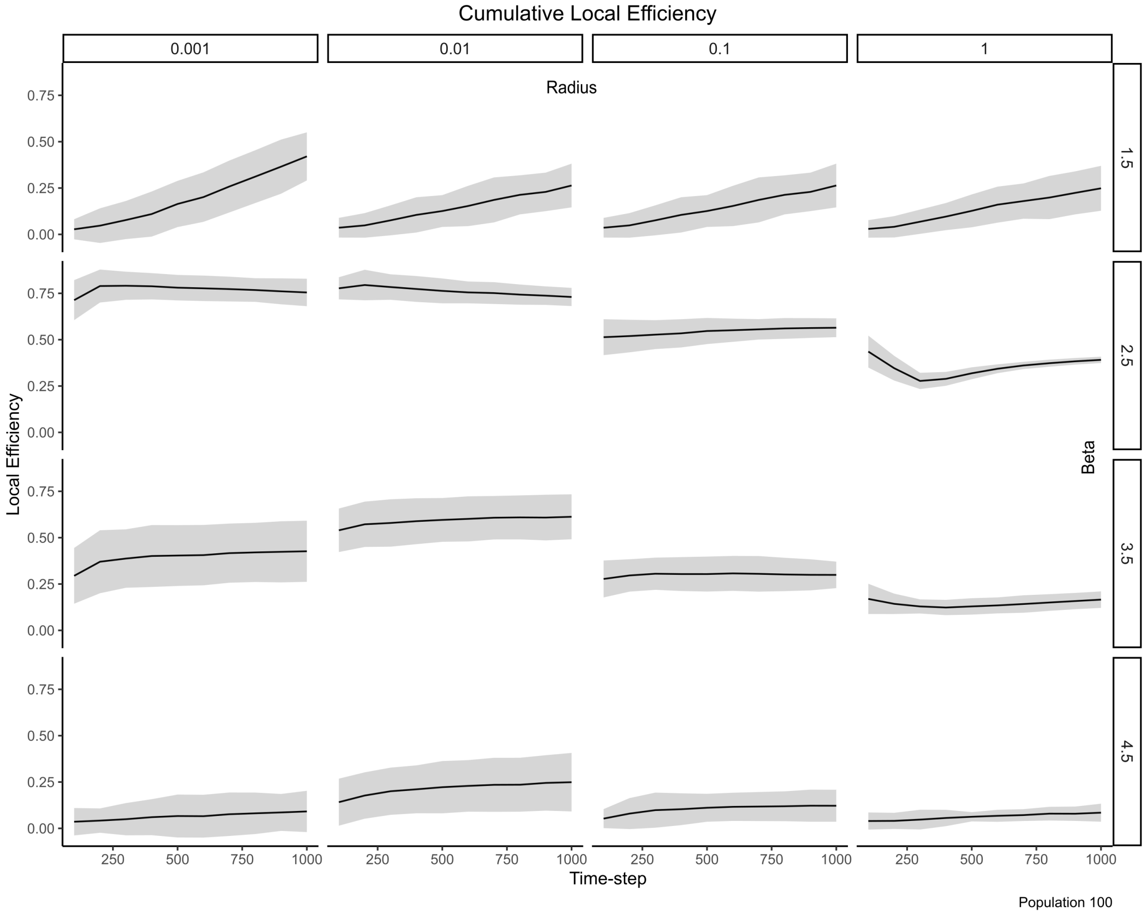

Figure C.5: Cumulative local efficiency for 1000 time-steps.

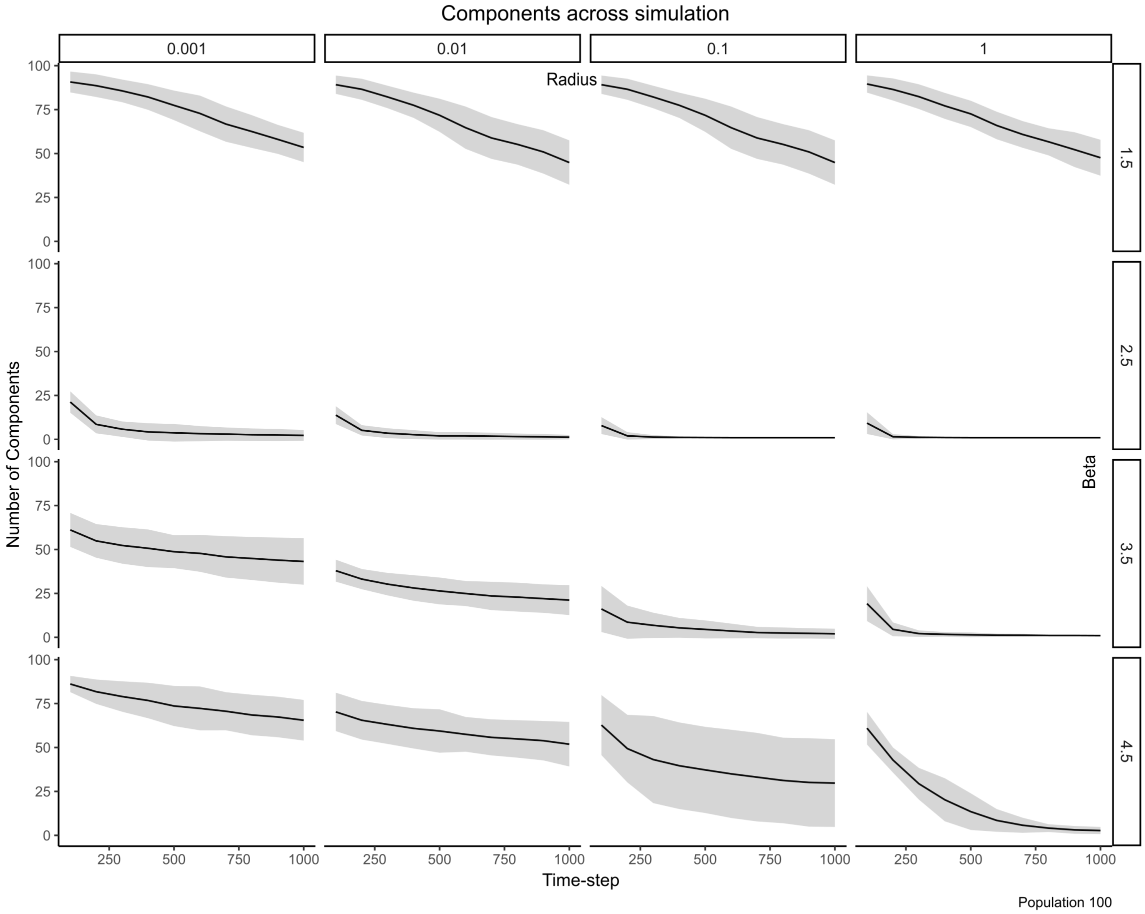

Figure C.6: Components per turn for 1000 time-steps.

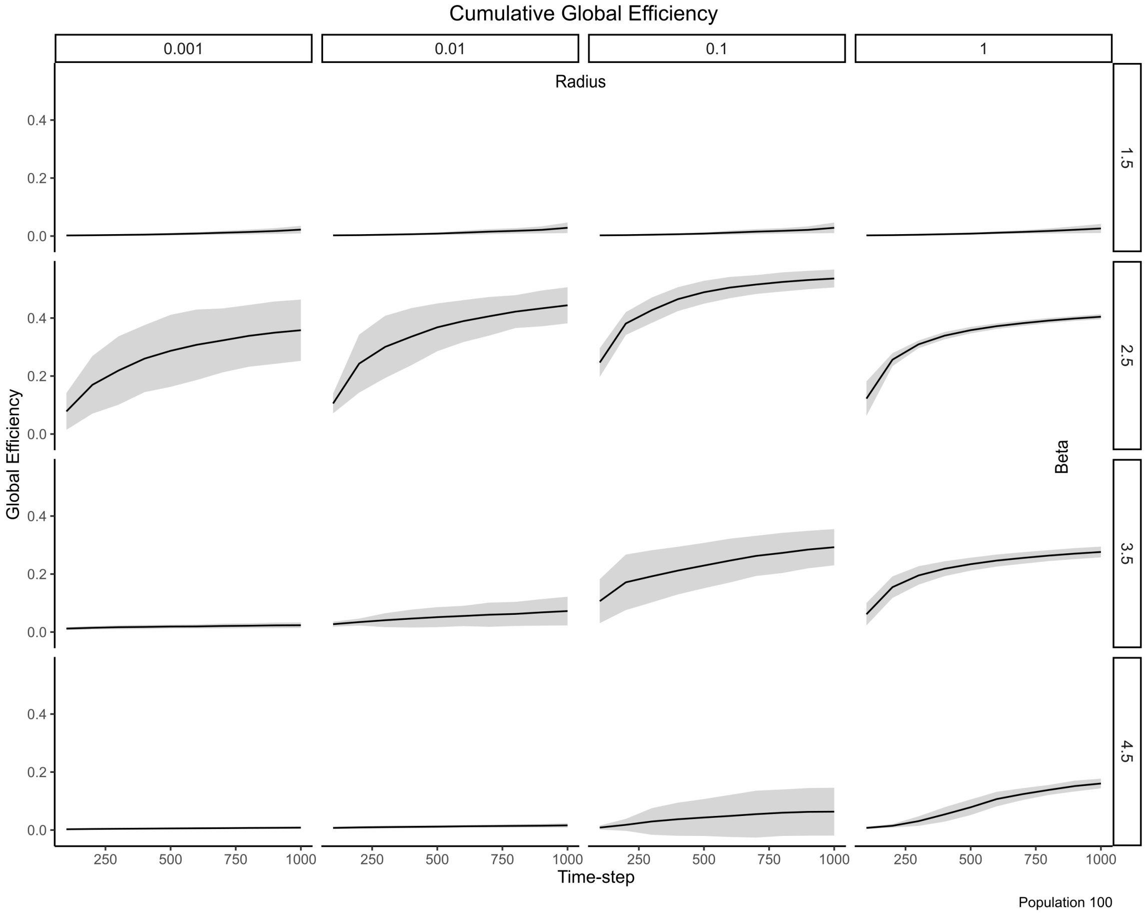

Figure C.7: Cumulative global efficiency for 1000 time-steps.

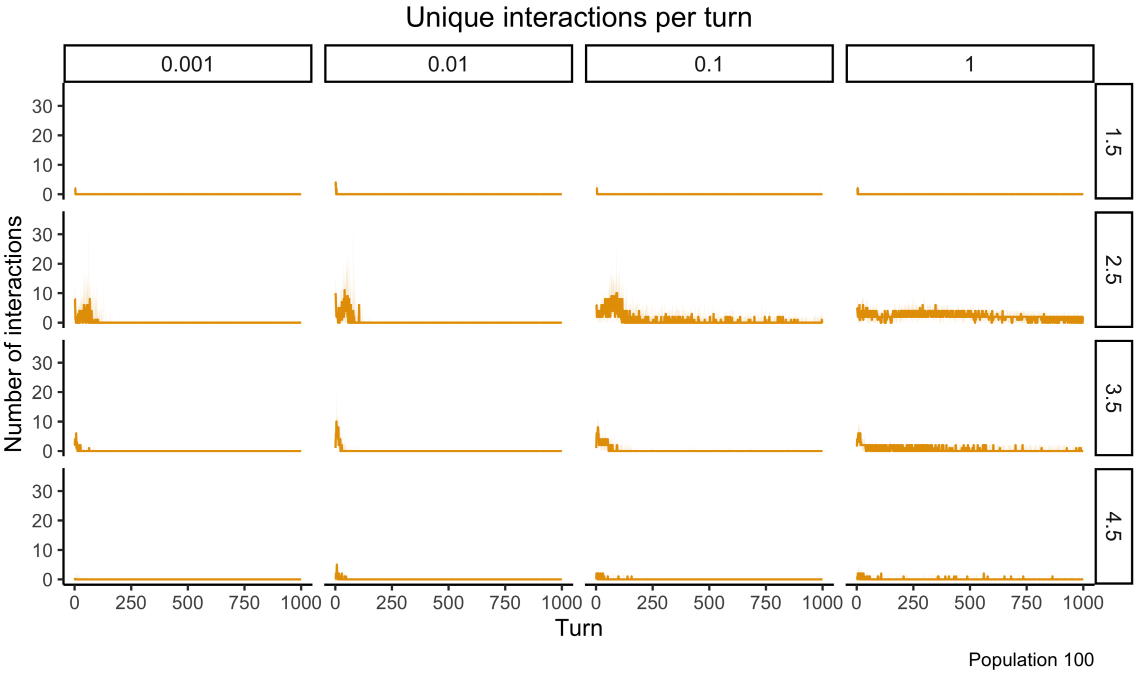

Figure C.8: Median of unique number of interactions per turn for 1000 time-steps.

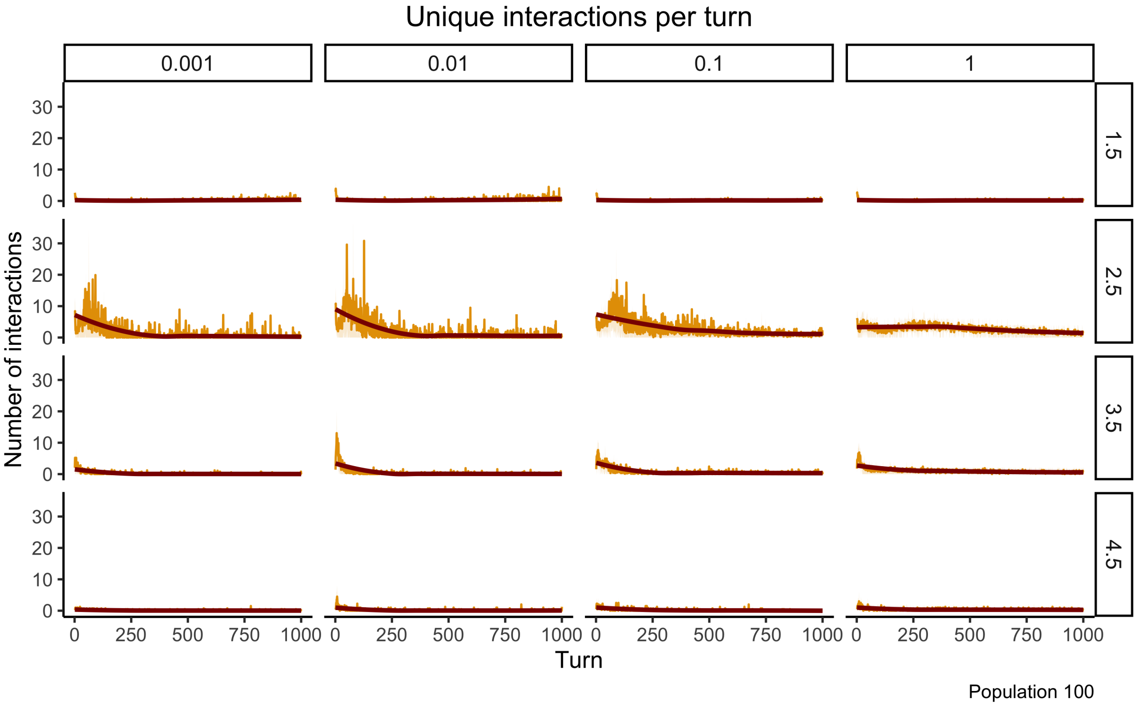

Figure C.9: Average number of unique interactions per turn for 1000 time-steps.

Bibliography

A. Acerbi, M. Smolla, and A. Mesoudi. Individual-based models of cultural evolution. 2020. URL `https://acerbialberto.com/IBM-cultevo/index.html#how-to-use-this-book---the-simulations`.

M. Afshar and L. A. Giraldeau. A unified modelling approach for producer-scrounger games in complex ecological conditions. *Animal Behaviour*, 96:167–176, 2014. ISSN 00033472. doi: 10.1016/j.anbehav.2014.07.022. URL `http://dx.doi.org/10.1016/j.anbehav.2014.07.022`.

E. Alden Smith. Anthropological applications of optimal foraging theory: a critical review with comment. *Current Anthropology*, 24(5):625–651, 1983. ISSN 00113204. doi: 10.1086/203066.

C. L. Apicella, F. W. Marlowe, J. H. Fowler, and N. A. Christakis. Social networks and cooperation in hunter-gatherers. *Nature*, 481(7382):497–501, 2012.

L. M. Aplin and J. Morand-Ferron. Stable producer–scrounger dynamics in wild birds: sociability and learning speed covary with scrounging behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 284(1852):20162872, 2017.

L. M. Aplin, D. R. Farine, R. P. Mann, and B. C. Sheldon. Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 2014. ISSN 14712954. doi: 10.1098/rspb.2014.1016.

M. Arbilly, U. Motro, M. W. Feldman, and A. Lotem. Evolution of social learning when high expected payoffs are associated with high risk of failure. *Journal of the Royal Society Interface*, 8(64):1604–1615, 2011.

F. Aureli, C. M. Schaffner, C. Boesch, S. K. Bearder, J. Call, C. A. Chapman, R. Connor, A. D. Fiore, R. I. Dunbar, S. P. Henzi, et al. Fission-fusion dynamics: new research frameworks. *Current Anthropology*, 49(4):627–654, 2008.

D. Barkoczi and M. Galesic. Social learning strategies modify the effect of network structure on group performance. *Nature Communications*, 7(1):1–8, 10 2016. ISSN 20411723. doi: 10.1038/ncomms13109. URL `www.nature.com/naturecommunications`.

C. J. Barnard and R. M. Sibly. Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29(2):543–550, 1981. ISSN 00033472. doi: 10.1016/S0003-3472(81)80117-0.

F. Bartumeus. Lévy processes in animal movement: An evolutionary hypothesis. *Fractals*, 15(2):151–162, 6 2007. ISSN 0218348X. doi: 10.1142/S0218348X07003460. URL `http://www.worldscientific.com/doi/abs/10.1142/S0218348X07003460`.

F. Bartumeus and S. A. Levin. Fractal reorientation clocks: Linking animal behavior to statistical patterns of search. Technical Report 49, 2008. URL `https://www.pnas.org/content/pnas/105/49/19072.full.pdf`.

F. Bartumeus, F. Peters, S. Pueyo, C. Marrasé, and J. Catalan. Helical Lévy walks: Adjusting searching statistics to resource availability in microzooplankton. *Proceedings of the National Academy of Sciences of the United States of America*, 100 (22):12771–12775, 2003. ISSN 00278424. doi: 10.1073/pnas.2137243100. URL `www.pnas.orgcgidoi10.1073pnas.2137243100`.

F. Bartumeus, M. G. Da Luz, G. M. Viswanathan, and J. Catalan. Animal search strategies: A quantitative random-walk analysis. *Ecology*, 86(11):3078–3087, 11 2005. ISSN 00129658. doi: 10.1890/04-1806. URL `http://doi.wiley.com/10.1890/04-1806`.

F. Bartumeus, P. Fernández, M. G. da Luz, J. Catalan, R. V. Solé, and S. A. Levin. Superdiffusion and encounter rates in diluted, low dimensional worlds. *European Physical Journal: Special Topics*, 157(1):157–166, 2008. ISSN 19516355. doi: 10.1140/epjst/e2008-00638-6. URL `https://link.springer.com/content/pdf/10.1140%2Fepjst%2Fe2008-00638-6.pdf`.

F. Bartumeus, E. P. Raposo, G. M. Viswanathan, and M. G. da Luz. Stochastic optimal foraging: tuning intensive and extensive dynamics in random searches. *PloS one*, 9(9):e106373, 2014.

F. Bartumeus, D. Campos, W. S. Ryu, R. Lloret-Cabot, V. Méndez, and J. Catalan. Foraging success under uncertainty: search tradeoffs and optimal space use. *Ecology Letters*, 19(11):1299–1313, 2016a. ISSN 14610248. doi: 10.1111/ele.12660. URL `https://onlinelibrary.wiley.com/doi/pdf/10.1111/ele.12660`.

F. Bartumeus, D. Campos, W. S. Ryu, R. Lloret-Cabot, V. Méndez, and J. Catalan. Foraging success under uncertainty: search tradeoffs and optimal space use. *Ecology letters*, 19(11):1299–1313, 2016b.

S. Bazazi, F. Bartumeus, J. J. Hale, and I. D. Couzin. Intermittent motion in desert locusts: Behavioural complexity in simple environments. *PLoS Computational Biology*, 8(5):e1002498, 5 2012. ISSN 1553734X. doi: 10.1371/journal.pcbi.1002498. URL `https://dx.plos.org/10.1371/journal.pcbi.1002498`.

G. Beauchamp. A spatial model of producing and scrounging. *Animal Behaviour*, 76(6):1935–1942, 2008. ISSN 00033472. doi: 10.1016/j.anbehav.2008.08.017. URL `http://dx.doi.org/10.1016/j.anbehav.2008.08.017`.

R. Beckers, J.-L. Deneubourg, S. Goss, and J. M. Pasteels. Collective decision making through food recruitment. *Insectes sociaux*, 37(3):258–267, 1990.

J. Beecham and K. Farnsworth. Animal group forces resulting from predator avoidance and competition minimization. *Journal of Theoretical Biology*, 198(4):533–548, 1999.

W. J. Bell. *Searching Behavior: the Behavioral Ecology of Finding Resources*. 1990. ISBN 9789401053723. doi: 10.1093/aesa/85.1.108.

S. Benhamou. How to reliably estimate the tortuosity of an animal's path: Straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, 229(2):209–220, 2004. ISSN 00225193. doi: 10.1016/j.jtbi.2004.03.016.

S. Benhamou. How many animals really do the lévy walk? *Ecology*, 88(8):1962–1969, 2007.

O. Bénichou, M. Coppey, M. Moreau, P. H. Suet, and R. Voituriez. Optimal search strategies for hidden targets. *Physical Review Letters*, 94(19), 2005. ISSN 00319007. doi: 10.1103/PhysRevLett.94.198101. URL `https://journals.aps.org/prl/pdf/10.1103/PhysRevLett.94.198101`.

O. Bénichou, C. Loverdo, M. Moreau, and R. Voituriez. Intermittent search strategies. *Reviews of Modern Physics*, 83(1):81–129, 2011. ISSN 00346861. doi: 10.1103/RevModPhys.83.81. URL `https://arxiv.org/pdf/1104.0639.pdf`.

E. Bernstein, J. Shore, and D. Lazer. How intermittent breaks in interaction improve collective intelligence. 115(35):8734–8739, 2018. doi: 10.7910/DVN/TSSQLY.

K. Bhattacharya and T. Vicsek. Collective foraging in heterogeneous landscapes. *Journal of the Royal Society Interface*, 11(100), 2014. ISSN 17425662. doi: 10.1098/rsif.2014.0674. URL `http://dx.doi.org/10.1098/rsif.2014.0674`.

S. Bikhchandani, D. Hirshleifer, and I. Welch. A theory of fads, fashion, custom, and cultural change as informational cascades. *Journal of political Economy*, 100(5):992–1026, 1992.

L. R. Binford. Willow Smoke and Dogs' Tails: Hunter-Gatherer Settlement Systems and Archaeological Site Formation. *American Antiquity*, 1980. ISSN 0002-7316. doi: 10.2307/279653.

L. R. Binford. *Constructing frames of reference: an analytical method for archaeological theory building using ethnographic and environmental data sets.* University of California Press, 2019.

D. W. Bird, R. B. Bird, B. F. Codding, and D. W. Zeanah. Variability in the organization and size of hunter-gatherer groups: Foragers do not live in small-scale societies. *Journal of Human Evolution*, 2019. ISSN 00472484. doi: 10.1016/j.jhevol.2019.03.005.

R. Bogacz, E. Brown, J. Moehlis, P. Holmes, and J. D. Cohen. The physics of optimal decision making: A formal analysis of models of performance in two-alternative forced-choice tasks. *Psychological Review*, 113(4):700–765, 2006. ISSN 0033295X. doi: 10.1037/0033-295X.113.4.700. URL `http://doi.apa.org/getdoi.cfm?doi=10.1037/0033-295X.113.4.700`.

A. B. Bond and A. C. Kamil. Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *Proceedings of the National Academy of Sciences of the United States of America*, 103(9):3214–3219, 2 2006. ISSN 00278424. doi: 10.1073/pnas.0509963103.

R. Bond. Group size and conformity. *Group processes & intergroup relations*, 8(4): 331–354, 2005.

R. Boyd and P. J. Richerson. *Culture and the evolutionary process.* University of Chicago Press, 1985.

R. Boyd and P. J. Richerson. Why does culture increase human adaptability? *Ethology and Sociobiology*, 1995. ISSN 01623095. doi: 10.1016/0162-3095(94)00073-G.

R. Boyd, P. J. Richerson, and J. Henrich. The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, 108(SUPPL. 2):10918–10925, 6 2011. ISSN 10916490. doi: 10.1073/pnas.1100290108. URL `www.pnas.org/cgi/doi/10.1073/pnas.1100290108`.

D. Boyer, O. Miramontes, G. Ramos-Fernández, J. L. Mateos, and G. Cocho. Modeling the searching behavior of social monkeys. *Physica A: Statistical Mechanics and its Applications*, 342(1-2 SPEC. ISS.):329–335, 2004. ISSN 03784371. doi: 10.1016/j.physa.2004.04.091. URL `www.elsevier.com/locate/physa`.

D. Boyer, M. C. Crofoot, and P. D. Walsh. Non-random walks in monkeys and humans. *Journal of the Royal Society Interface*, 9(70):842–847, 2012. ISSN 17425662. doi: 10.1098/rsif.2011.0582.

C. Bracis, E. Gurarie, B. Van Moorter, and R. A. Goodwin. Memory effects on movement behavior in animal foraging. *PLoS ONE*, 10(8): e0136057, 8 2015. ISSN 19326203. doi: 10.1371/journal.pone.0136057. URL `http://www.ncbi.nlm.nih.gov/pubmed/26288228http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC4542208https://dx.plos.org/10.1371/journal.pone.0136057`.

P. J. Brantingham, J. Eerkens, J. Féblot-Augustins, J. Haws, M. Shott, P. Turchin, and H. van Gijseghem. Measuring forager mobility. *Current Anthropology*, 47 (3):435–459, 6 2006. ISSN 00113204. doi: 10.1086/503062. URL `https://www.journals.uchicago.edu/doi/abs/10.1086/503062`.

A. S. Brooks, J. E. Yellen, R. Potts, A. K. Behrensmeyer, A. L. Deino, D. E. Leslie, S. H. Ambrose, J. R. Ferguson, F. d'Errico, A. M. Zipkin, et al. Long-distance stone transport and pigment use in the earliest middle stone age. *Science*, 360 (6384):90–94, 2018.

C. Brown, K. Laland, and J. Krause. *Fish cognition and behavior*, volume 21. John Wiley & Sons, 2011.

C. T. Brown, L. S. Liebovitch, and R. Glendon. Lévy flights in dobe Ju/'hoansi foraging patterns. *Human Ecology*, 35(1):129–138, 2007. ISSN 03007839. doi: 10.1007/s10745-006-9083-4.

D. Campos, V. Méndez, and F. Bartumeus. Optimal intermittence in search strategies under speed-selective target detection. *Physical Review Letters*, 108(2):028102, 1 2012. ISSN 00319007. doi: 10.1103/PhysRevLett.108.028102.

M. Cantor, L. G. Shoemaker, R. B. Cabral, C. O. Flores, M. Varga, and H. Whitehead. Multilevel animal societies can emerge from cultural transmission. *Nature communications*, 6(1):1–10, 2015.

T. Caraco and L.-A. Giraldea. Social foraging: producing and scrounging in a stochastic environment. *Journal of Theoretical Biology*, 153(4):559–583, 1991.

M. Cartmill, D. Pilbeam, and G. Isaac. One hundred years of paleoanthropology. *American Scientist*, 1986. ISSN 00030996.

D. Centola. The spread of behavior in an online social network experiment. *Science*, 2010. ISSN 10959203. doi: 10.1126/science.1185231.

E. L. Charnov. Optimal foraging, the marginal value theorem. *Theoretical population biology*, 9(2):129–136, 1976.

E. L. Charnov and others. Optimal foraging, the marginal value theorem. 1976.

L. Chittka and N. E. Raine. Recognition of flowers by pollinators, 8 2006. ISSN 13695266.

L. Chittka, P. Skorupski, and N. E. Raine. Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology and Evolution*, 24(7):400–407, 2009. ISSN 01695347. doi: 10.1016/j.tree.2009.02.010.

C. W. Clark and M. Mangel. The evolutionary advantages of group foraging. *Theoretical Population Biology*, 30(1):45–75, 8 1986. ISSN 10960325. doi: 10.1016/0040-5809(86)90024-9.

A. Clauset, C. R. Shalizi, and M. E. Newman. Power-law distributions in empirical data. *SIAM Review*, 51(4):661–703, 2009. ISSN 00361445. doi: 10.1137/070710111. URL `http://epubs.siam.org/doi/10.1137/070710111`.

M. Collard, A. Ruttle, B. Buchanan, and M. J. O'Brien. Population Size and Cultural Evolution in Nonindustrial Food-Producing Societies. *PLoS ONE*, 2013. ISSN 19326203. doi: 10.1371/journal.pone.0072628.

I. Coolen. Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (lonchura punctulata). *Behavioral Ecology and Sociobiology*, 52(3):232–238, 2002.

I. D. Couzin. Collective cognition in animal groups. *Trends in Cognitive Sciences*, 13 (1):36–43, 2009. ISSN 13646613. doi: 10.1016/j.tics.2008.10.002.

N. Creanza, O. Kolodny, and M. W. Feldman. Greater than the sum of its parts? Modelling population contact and interaction of cultural repertoires. *Journal of the Royal Society Interface*, 2017. ISSN 17425662. doi: 10.1098/rsif.2017.0171.

M. G. E. Da Luz, E. P. Raposo, and G. M. Viswanathanc. Subjective expectation of rewards can change the behavior of smart but impatient foragers. *Proceedings of the National Academy of Sciences of the United States of America*, 113(31):8571–8573, 7 2016. ISSN 10916490. doi: 10.1073/pnas.1609369113. URL `http://www.ncbi.nlm.nih.gov/pubmed/27444011http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC4978234`.

S. R. Dall, L.-A. Giraldeau, O. Olsson, J. M. McNamara, and D. W. Stephens. Information and its use by animals in evolutionary ecology. *Trends in ecology & evolution*, 20(4):187–193, 2005.

A. J. de Froment, D. I. Rubenstein, and S. A. Levin. An Extra Dimension to Decision-Making in Animals: The Three-way Trade-off between Speed, Effort per-Unit-Time and Accuracy. *PLoS Computational Biology*, 10(12):e1003937, 12 2014. ISSN 15537358. doi: 10.1371/journal.pcbi.1003937. URL `http://dx.plos.org/10.1371/journal.pcbi.1003937`.

F. X. Dechaume-Moncharmont, A. Dornhaus, A. I. Houston, J. M. McNamara, E. J. Collins, and N. R. Franks. The hidden cost of information in collective foraging.

Proceedings of the Royal Society B: Biological Sciences, 272(1573):1689–1695, 2005. ISSN 14712970. doi: 10.1098/rspb.2005.3137.

M. Derex and R. Boyd. Partial connectivity increases cultural accumulation within groups. *Proceedings of the National Academy of Sciences of the United States of America*, 113(11):2982–2987, 3 2016a. ISSN 10916490. doi: 10.1073/pnas.1518798113. URL `www.pnas.org/cgi/doi/10.1073/pnas.1518798113`.

M. Derex and R. Boyd. Partial connectivity increases cultural accumulation within groups. *Proceedings of the National Academy of Sciences*, 113(11):2982–2987, 2016b.

C. Detrain and J.-L. Deneubourg. Self-organized structures in a superorganism: do ants "behave" like molecules? *Physics of life Reviews*, 3(3):162–187, 2006.

M. S. Di Bitetti and C. H. Janson. Social foraging and the finder's share in capuchin monkeys, cebus apella. *Animal Behaviour*, 62(1):47–56, 2001.

S. S. Ding, L. S. Muhle, A. E. X. Brown, L. J. Schumacher, and R. G. Endres. Comparison of solitary and collective foraging strategies of Caenorhabditis elegans in patchy food distributions . *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1807):20190382, 2020. ISSN 0962-8436. doi: 10.1098/rstb.2019.0382. URL `https://royalsocietypublishing.org/doi/abs/10.1098/rstb.2019.0382?af=R&utm_source=researcher_app&utm_medium=referral&utm_campaign=RESR_MRKT_Researcher_inbound`.

N. J. Dingemanse, C. Both, A. J. Van Noordwijk, A. L. Rutten, and P. J. Drent. Natal dispersal and personalities in great tits (parus major). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1516):741–747, 2003.

M. C. Donaldson-Matasci and A. Dornhaus. How habitat affects the benefits of communication in collectively foraging honey bees. *Behavioral Ecology and Sociobiology*, 66(4):583–592, 2012.

A. Dornhaus and L. Chittka. Information flow and regulation of foraging activity in bumble bees (bombus spp.). *Apidologie*, 35(2):183–192, 2004.

R. Dukas. Causes and consequences of limited attention. *Brain, Behavior and Evolution*, 63(4):197–210, 2004. ISSN 00068977. doi: 10.1159/000076781.

M. Dumke, M. E. Herberstein, and J. M. Schneider. Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider. *Proceedings of the Royal Society B: Biological Sciences*, 283(1828):20160114, 2016.

M. Dyble. The effect of dispersal on rates of cumulative cultural evolution. *Biology Letters*, 2018. ISSN 1744957X. doi: 10.1098/rsbl.2018.0069.

M. Dyble, G. D. Salali, N. Chaudhary, A. Page, D. Smith, J. Thompson, L. Vinicius, R. Mace, and A. B. Migliano. Sex equality can explain the unique social structure of hunter-gatherer bands. *Science*, 2015. ISSN 10959203. doi: 10.1126/science.aaa5139.

J. R. Dyer, D. P. Croft, L. J. Morrell, and J. Krause. Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20(1):165–171, 2009.

K. Egert-Berg, E. R. Hurme, S. Greif, A. Goldstein, L. Harten, J. J. Flores-Martínez, A. T. Valdés, D. S. Johnston, O. Eitan, I. Borissov, et al. Resource ephemerality drives social foraging in bats. *Current Biology*, 28(22):3667–3673, 2018.

C. Fang, J. Lee, and M. A. Schilling. Balancing exploration and exploitation through structural design: The isolation of subgroups and organizational learning. *Organization Science*, 21(3):625–642, 2010.

K. D. Farnsworth and J. A. Beecham. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. *American Naturalist*, 153(5):509–526, 1999. ISSN 00030147. doi: 10.1086/303192.

J. Ferreira, E. Raposo, H. Araújo, M. da Luz, G. Viswanathan, F. Bartumeus, and D. Campos. Landscape-scaled strategies can outperform lévy random searches. *Physical Review E*, 103(2):022105, 2021.

S. Focardi, P. Montanaro, and E. Pecchioli. Adaptive Lévy walks in foraging fallow deer. *PLoS ONE*, 4(8):e6587, 8 2009. ISSN 19326203. doi: 10.1371/journal.pone.0006587. URL `http://dx.plos.org/10.1371/journal.pone.0006587`.

R. Foley and C. Gamble. The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2009. ISSN 14712970. doi: 10.1098/rstb.2009.0136.

R. B. Freeman and W. Huang. Collaboration: Strength in diversity. *Nature*, 513 (7518):305–305, 2014.

B. G. Galef and K. N. Laland. Social learning in animals: empirical studies and theoretical models. *Bioscience*, 55(6):489–499, 2005.

R. R. Gameiro, K. Kaspar, S. U. König, S. Nordholt, and P. König. Exploration and Exploitation in Natural Viewing Behavior. *Scientific Reports*, 7(1):1–23, 2017. ISSN 20452322. doi: 10.1038/s41598-017-02526-1.

K. Garg and C. T. Kello. Efficient Lévy walks in virtual human foraging. *Scientific Reports*, 11(1):5242, 12 2021. ISSN 20452322. doi: 10.1038/s41598-021-84542-w. URL `https://www.nature.com/articles/s41598-021-84542-w`.

K. Garg, C. Padilla-Iglesias, N. Restrepo Ochoa, and V. B. Knight. Hunter–gatherer foraging networks promote information transmission. *Royal Society open science*, 8(12):211324, 2021.

K. Garg, C. T. Kello, and P. E. Smaldino. Individual exploration and selective social learning: Balancing exploration-exploitation trade-offs in collective foraging. *Journal of the Royal Society Interface*, 19(189):20210915, 2022.

G. Gigerenzer. *Heuristics - The foundations of adaptive behavior.* 2011. ISBN 9780199744282.

G. Gigerenzer and T. Sturm. How (far) can rationality be naturalized? *Synthese*, 187(1):243–268, 2012.

L. A. Giraldeau. Group foraging: the skill pool effect and frequency-dependent learning. *American Naturalist*, 124(1):72–79, 1984. ISSN 00030147. doi: 10.1086/284252.

L.-A. Giraldeau and T. Caraco. *Social foraging theory*. Princeton University Press, 2018.

L.-A. Giraldeau, T. J. Valone, and J. J. Templeton. Potential disadvantages of using socially acquired information. 2002. doi: 10.1098/rstb.2002.1065.

L.-A. Giraldeau, P. Heeb, and M. Kosfeld. *Investors and Exploiters in Ecology and Economics: Principles and Applications*, volume 21. MIT Press, 2017.

R. L. Goldstone and T. M. Gureckis. Collective behavior. *Topics in cognitive science*, 1(3):412–438, 2009.

R. L. Goldstone, T. N. Wisdom, M. E. Roberts, and S. Frey. Learning Along With Others. In *Psychology of Learning and Motivation - Advances in Research and Theory*, volume 58, pages 1–45. Academic Press Inc., 1 2013. doi: 10.1016/B978-0-12-407237-4.00001-3.

C. J. Gomez and D. M. Lazer. Clustering knowledge and dispersing abilities enhances collective problem solving in a network. *Nature Communications*, 10(1):1–11, 12 2019. ISSN 20411723. doi: 10.1038/s41467-019-12650-3. URL `https://doi.org/10.1038/s41467-019-12650-3`.

M. Grove. Hunter-gatherer movement patterns: Causes and constraints. *Journal of Anthropological Archaeology*, 2009. ISSN 10902686. doi: 10.1016/j.jaa.2009.01.003.

M. Grove. Population density, mobility, and cultural transmission. *Journal of Archaeological Science*, 2016. ISSN 10959238. doi: 10.1016/j.jas.2016.09.002.

M. Grove. Hunter-gatherers adjust mobility to maintain contact under climatic variation. *Journal of Archaeological Science: Reports*, 2018. ISSN 2352409X. doi: 10.1016/j.jasrep.2018.04.003.

M. Grove and R. Dunbar. Local objects, distant symbols: fission-fusion social systems and the evolution of human cognition. 2015.

M. Grove, S. J. Lycett, and P. R. Chauhan. *The Quantitative Analysis of Mobility: Ecological Techniques and Archaeological Extensions*. 2010. ISBN 9781441968609. doi: 10.1007/978-1-4419-6861-6.

M. Grove, E. Pearce, and R. I. Dunbar. Fission-fusion and the evolution of hominin social systems. *Journal of Human Evolution*, 2012a. ISSN 00472484. doi: 10.1016/j.jhevol.2011.10.012.

M. Grove, E. Pearce, and R. I. Dunbar. Fission-fusion and the evolution of hominin social systems. *Journal of Human Evolution*, 62(2):191–200, 2 2012b. ISSN 00472484. doi: 10.1016/j.jhevol.2011.10.012.

C. Grueter and E. Leadbeater. Insights from insects about adaptive social information use. *Trends in ecology & evolution*, 29(3):177–184, 2014.

C. C. Grueter and D. R. White. On the emergence of large-scale human social integration and its antecedents in primates. *Structure and Dynamics*, 7(1), 2014.

C. C. Grueter, X. Qi, D. Zinner, T. Bergman, M. Li, Z. Xiang, P. Zhu, A. B. Migliano, A. Miller, M. Krützen, J. Fischer, D. I. Rubenstein, T. N. Vidya, B. Li, M. Cantor, and L. Swedell. Multilevel Organisation of Animal Sociality, 2020. ISSN 01695347.

C. Grüter and E. Leadbeater. Insights from insects about adaptive social information use. *Trends in Ecology and Evolution*, 29(3):177–184, 2014. ISSN 01695347. doi: 10.1016/j.tree.2014.01.004.

C. Grüter, M. S. Balbuena, and W. M. Farina. Informational conflicts created by the waggle dance. *Proceedings of the Royal Society B: Biological Sciences*, 275(1640): 1321–1327, 2008.

M. J. Hamilton, B. T. Milne, R. S. Walker, O. Burger, and J. H. Brown. The complex structure of hunter–gatherer social networks. *Proceedings of the Royal Society B: Biological Sciences*, 274(1622):2195–2203, 2007.

M. J. Hamilton, J. Lobo, E. Rupley, H. Youn, and G. B. West. The ecological and evolutionary energetics of hunter-gatherer residential mobility. *Evolutionary Anthropology*, 25(3):124–132, 2016. ISSN 15206505. doi: 10.1002/evan.21485.

M. J. Hamilton, B. Buchanan, and R. S. Walker. SCALING the SIZE, STRUCTURE, and DYNAMICS of RESIDENTIALLY MOBILE HUNTER-GATHERER CAMPS. *American Antiquity*, 2018a. ISSN 00027316. doi: 10.1017/aaq.2018.39.

M. J. Hamilton, B. Buchanan, and R. S. Walker. Scaling the size, structure, and dynamics of residentially mobile hunter-gatherer camps. *American Antiquity*, 83 (4):701–720, 2018b.

R. Harpaz and E. Schneidman. Social interactions drive efficient foraging and income equality in groups of fish. *Elife*, 9:e56196, 2020.

Y. Hart, H. Goldberg, E. Striem-Amit, A. E. Mayo, L. Noy, and U. Alon. Creative exploration as a scale-invariant search on a meaning landscape. *Nature Communications*, 9(1):5411, 12 2018. ISSN 20411723. doi: 10.1038/s41467-018-07715-8. URL `http://www.nature.com/articles/s41467-018-07715-8`.

P. He, A. A. Maldonado-Chaparro, and D. R. Farine. The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behavioral Ecology and Sociobiology*, 73(1):1–14, 2019.

A. M. Hein and S. A. McKinley. Sensing and decision-making in random search. *Proceedings of the National Academy of Sciences of the United States of America*, 109(30):12070–12074, 2012. ISSN 00278424. doi: 10.1073/pnas.1202686109. URL `https://www.pnas.org/content/pnas/109/30/12070.full.pdf`.

J. Henrich. Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the tasmanian case. *American antiquity*, pages 197–214, 2004.

I. Herbinger, C. Boesch, and H. Rothe. Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology*, 2001. ISSN 01640291. doi: 10.1023/A:1005663212997.

C. Heyes. Blackboxing: social learning strategies and cultural evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1693):20150369, 2016.

K. Hill, M. Barton, and A. M. Hurtado. The emergence of human uniqueness: Characters underlying behavioral modernity. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 18(5):187–200, 2009.

K. R. Hill, R. S. Walker, M. Božičević, J. Eder, T. Headland, B. Hewlett, A. M. Hurtado, F. Marlowe, P. Wiessner, and B. Wood. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, 2011. ISSN 00368075. doi: 10.1126/science.1199071.

K. R. Hill, B. M. Wood, J. Baggio, A. M. Hurtado, and R. T. Boyd. Hunter-gatherer inter-band interaction rates: Implications for cumulative culture. *PLoS ONE*, 2014. ISSN 19326203. doi: 10.1371/journal.pone.0102806.

T. Hills. Animal foraging and the evolution of goal-directed cognition. *Cognitive Science*, 30(1):3–41, 1 2006. ISSN 03640213. doi: 10.1207/s15516709cog0000{_}50. URL `http://doi.wiley.com/10.1207/s15516709cog0000_50`.

T. T. Hills, M. N. Jones, and P. M. Todd. Optimal foraging in semantic memory. *Psychological Review*, 119(2):431–440, 2012. ISSN 0033295X. doi: 10.1037/a0027373.

T. T. Hills, P. M. Todd, D. Lazer, A. D. Redish, I. D. Couzin, C. S. R. Group, et al. Exploration versus exploitation in space, mind, and society. *Trends in cognitive sciences*, 19(1):46–54, 2015.

D. J. Hoare, I. D. Couzin, J.-G. Godin, and J. Krause. Context-dependent group size choice in fish. *Animal Behaviour*, 67(1):155–164, 2004.

B. Hölldobler, E. O. Wilson, et al. *The ants*. Harvard University Press, 1990.

L. Hong and S. E. Page. Groups of diverse problem solvers can outperform groups of high-ability problem solvers. *Proceedings of the National Academy of Sciences of the United States of America*, 101(46):16385–16389, 11 2004. ISSN 00278424. doi: 10.1073/pnas.0403723101. URL `www.pnas.orgcgidoi10.1073pnas.0403723101`.

V. Horner and A. Whiten. Causal knowledge and imitation/emulation switching in chimpanzees (pan troglodytes) and children (homo sapiens). *Animal cognition*, 8 (3):164–181, 2005.

E. Hovers and A. Belfer-Cohen. “Now You See it, Now You Don’t”—Modern Human Behavior in the Middle Paleolithic. In *Transitions Before the Transition*. 2006. doi: 10.1007/0-387-24661-4_16.

N. E. Humphries and D. W. Sims. Optimal foraging strategies: Lévy walks balance searching and patch exploitation under a very broad range of conditions. *Journal of Theoretical Biology*, 358:179–193, 10 2014. ISSN 10958541. doi: 10.1016/j.jtbi.2014.05.032. URL `http://www.ncbi.nlm.nih.gov/pubmed/24882791`.

N. E. Humphries, N. Queiroz, J. R. Dyer, N. G. Pade, M. K. Musyl, K. M. Schaefer, D. W. Fuller, J. M. Brunnschweiler, T. K. Doyle, J. D. Houghton, et al. Environmental context explains lévy and brownian movement patterns of marine predators. *Nature*, 465(7301):1066–1069, 2010.

C. C. Ioannou and S. R. Dall. Individuals that are consistent in risk-taking benefit during collective foraging. *Scientific reports*, 6(1):1–9, 2016.

G. Isaac. The food-sharing behavior of protohuman hominids. *Scientific American*, 1978. ISSN 00368733. doi: 10.1038/scientificamerican0478-90.

R. Jagiello, C. Heyes, and H. Whitehouse. Tradition and invention: The bifocal stance theory of cultural evolution. *Behavioral and Brain Sciences*, pages 1–50, 2022.

H. Jang, C. Boesch, R. Mundry, S. D. Ban, and K. R. Janmaat. Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. *Scientific Reports*, 2019. ISSN 20452322. doi: 10.1038/s41598-019-47247-9.

R. A. Johnstone and A. Manica. Evolution of personality differences in leadership. *Proceedings of the National Academy of Sciences*, 108(20):8373–8378, 2011.

J. W. Jolles, A. Fleetwood-Wilson, S. Nakayama, M. C. Stumpe, R. A. Johnstone, and A. Manica. The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks. *Animal Behaviour*, 99:147–153, 2015.

C. Kalff and T. Hills. Human foraging behavior : A virtual reality investigation on area restricted search in humans. *Search*, 32(32):168–173, 2006. URL `https://cloudfront.escholarship.org/dist/prd/content/qt74m6d4qr/qt74m6d4qr.pdf`.

T. Kameda and D. Nakanishi. Cost-benefit analysis of social/cultural learning in a nonstationary uncertain environment. An evolutionary simulation and an experiment with human subjects. *Evolution and Human Behavior*, 23(5):373–393, 2002. ISSN 10905138. doi: 10.1016/S1090-5138(02)00101-0.

A. C. Kamil, Krebs J. R., and H. R. Pulliam. *Foraging Behavior*. 1987. ISBN 9781461290278. doi: 10.1007/978-1-4613-1839-2.

P. Kareiva and G. Odell. Swarms of predators exhibit" preytaxis" if individual predators use area-restricted search. *The American Naturalist*, 130(2):233–270, 1987.

M. Kaushal. Divining the Landscape—the Gaddi and his land. *India International Centre Quarterly*, 27:31–40, 2001.

R. L. Kelly. Hunter-Gatherer Mobility Strategies. *Journal of Anthropological Research*, 1983. ISSN 0091-7710. doi: 10.1086/jar.39.3.3629672.

R. L. Kelly. Mobility. In *The Lifeways of Hunter-Gatherers: The Foraging Spectrum*, page 77–113. Cambridge University Press, 2013. doi: 10.1017/CBO9781139176132.005.

J. M. Kembro, M. Lihoreau, J. Garriga, E. P. Raposo, and F. Bartumeus. Bumblebees learn foraging routes through exploitation–exploration cycles. *Journal of the Royal Society Interface*, 16(156):20190103, 2019.

J. Kendal, L. A. Giraldeau, and K. Laland. The evolution of social learning rules: Payoff-biased and frequency-dependent biased transmission. *Journal of Theoretical Biology*, 260(2):210–219, 9 2009. ISSN 00225193. doi: 10.1016/j.jtbi.2009.05.029.

R. L. Kendal, I. Coolen, Y. van Bergen, and K. N. Laland. Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, 35:333–379, 2005.

R. L. Kendal, N. J. Boogert, L. Rendell, K. N. Laland, M. Webster, and P. L. Jones. Social Learning Strategies: Bridge-Building between Fields. *Trends in Cognitive Sciences*, 22(7):651–665, 2018. ISSN 1879307X. doi: 10.1016/j.tics.2018.04.003. URL `https://doi.org/10.1016/j.tics.2018.04.003`.

B. E. Kerster, T. Rhodes, and C. T. Kello. Spatial memory in foraging games. *Cognition*, 148:85–96, 2016a. ISSN 18737838. doi: 10.1016/j.cognition.2015.12.015. URL `http://dx.doi.org/10.1016/j.cognition.2015.12.015`.

B. E. Kerster, T. Rhodes, and C. T. Kello. Spatial memory in foraging games. *Cognition*, 148:85–96, 2016b.

A. Kölzsch, A. Alzate, F. Bartumeus, M. De Jager, E. J. Weerman, G. M. Hengeveld, M. Naguib, B. A. Nolet, and J. Van De Koppel. Experimental evidence for inherent lévy search behaviour in foraging animals. *Proceedings of the Royal Society B: Biological Sciences*, 282(1807):20150424, 5 2015. ISSN 14712954. doi: 10.1098/rspb.2015.0424. URL `https://royalsocietypublishing.org/doi/10.1098/rspb.2015.0424`.

W. Kool and M. Botvinick. Mental labour. *Nature human behaviour*, 2(12):899–908, 2018.

C. W. Korn and D. R. Bach. Heuristic and optimal policy computations in the human brain during sequential decision-making. *Nature Communications*, 9(1):1–15, 12 2018. ISSN 20411723. doi: 10.1038/s41467-017-02750-3. URL `www.nature.com/naturecommunications`.

C. Y. Kouakou, C. Boesch, and H. S. Kuehl. Identifying hotspots of chimpanzee group activity from transect surveys in Taï National Park, Côte d'Ivoire. *Journal of Tropical Ecology*, 2011. ISSN 14697831. doi: 10.1017/S0266467411000423.

D. L. Kramer and R. L. McLaughlin. The Behavioral Ecology of Intermittent Locomotion. *American Zoologist*, 41(2):137–153, 4 2001. ISSN 0003-1569. doi: 10.1093/icb/41.2.137. URL `https://academic.oup.com/icb/article-lookup/doi/10.1093/icb/41.2.137`.

J. R. Krebs, A. Kacelnik, and P. Taylor. Test of optimal sampling by foraging great tits. *Nature*, 275(5675):27–31, 1978. ISSN 00280836. doi: 10.1038/275027a0.

J. R. Krebs, D. W. Stephens, W. J. Sutherland, et al. *Perspectives in optimal foraging.* Cambridge University Press Cambridge, 1983.

S. L. Kuhn. Moving on from here: Suggestions for the future of "mobility thinking" in studies of paleolithic technologies. *Journal of Paleolithic Archaeology*, pages 1–18, 2020.

S. L. Kuhn, D. A. Raichlen, and A. E. Clark. What moves us? How mobility and movement are at the center of human evolution. *Evolutionary anthropology*, 25(3):86–97, may 2016. ISSN 15206505. doi: 10.1002/evan.21480. URL `http://doi.wiley.com/10.1002/evan.21480`.

R. H. Kurvers, B. Eijkelenkamp, K. van Oers, B. van Lith, S. E. van Wieren, R. C. Ydenberg, and H. H. Prins. Personality differences explain leadership in barnacle geese. *Animal Behaviour*, 78(2):447–453, 2009.

R. H. Kurvers, H. H. Prins, S. E. Van Wieren, K. Van Oers, B. A. Nolet, and R. C. Ydenberg. The effect of personality on social foraging: Shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences*, 277(1681):601–608, 2010. ISSN 14712970. doi: 10.1098/rspb.2009.1474.

K. Laland and A. Seed. Understanding human cognitive uniqueness. *Annual Review of Psychology*, 72:689–716, 2021.

K. N. Laland. Social learning strategies. *Animal Learning & Behavior*, 32(1):4–14, 2004.

K. N. Laland, N. Atton, and M. M. Webster. From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567):958–968, 2011.

D. E. LaScala-Gruenewald, R. S. Mehta, Y. Liu, and M. W. Denny. Sensory perception plays a larger role in foraging efficiency than heavy-tailed movement strategies. *Ecological Modelling*, 404(October 2018):69–82, 2019. ISSN 03043800. doi: 10.1016/j.ecolmodel.2019.02.015. URL `https://doi.org/10.1016/j.ecolmodel.2019.02.015`.

V. Latora and M. Marchiori. Efficient behavior of small-world networks. *Physical Review Letters*, 2001. ISSN 10797114. doi: 10.1103/PhysRevLett.87.198701.

R. Layton and S. O'Hara. Human social evolution: a comparison of hunter-gatherer and chimpanzee social organization. 2010.

R. Layton and S. O'Hara. Human Social Evolution: A Comparison of Hunter-gatherer and Chimpanzee Social Organization. In *Social Brain, Distributed Mind*. 2012. ISBN 9780191734724. doi: 10.5871/bacad/9780197264522.003.0005.

D. Lazer and A. Friedman. The Network Structure of Exploration and Exploitation. Technical report, 2007.

E. Leadbeater and L. Chittka. The dynamics of social learning in an insect model, the bumblebee (bombus terrestris). *Behavioral Ecology and Sociobiology*, 61(11): 1789–1796, 2007.

J. Lehmann, P. Lee, and R. Dunbar. Unravelling the function of communitylevel organization. *Lucy to language: the benchmark papers*, 245, 2014.

N. J. Lemanski, C. N. Cook, C. Ozturk, B. H. Smith, and N. Pinter-Wollman. The effect of individual learning on collective foraging in honey bees in differently structured landscapes. *Animal Behaviour*, 179:113–123, 2021.

S. A. Levin. The problem of pattern and scale in ecology. *Ecology*, 73(6):1943–1967, 1992. ISSN 00129658. doi: 10.2307/1941447.

H. M. Lewis, L. Vinicius, J. Strods, R. MacE, and A. B. Migliano. High mobility explains demand sharing and enforced cooperation in egalitarian hunter-gatherers. *Nature Communications*, 5:1–8, 2014. ISSN 20411723. doi: 10.1038/ncomms6789.

C. List, C. Elsholtz, and T. D. Seeley. Independence and interdependence in collective decision making: An agent-based model of nest-site choice by honeybee swarms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1518): 755–762, 3 2009. ISSN 14712970. doi: 10.1098/rstb.2008.0277. URL `https://royalsocietypublishing.org/`.

M. Luthra and P. M. Todd. Social search evolves with the emergence of clustered environments. In *ALIFE 2021: The 2021 Conference on Artificial Life*. MIT Press, 2021.

J. G. March. Exploration and exploitation in organizational learning. *Organization science*, 2(1):71–87, 1991.

F. W. Marlowe. Hunter-gatherers and human evolution, 2005. ISSN 10601538.

R. Martínez-García, J. M. Calabrese, T. Mueller, K. A. Olson, and C. López. Optimizing the search for resources by sharing information: Mongolian gazelles as a case study. *Physical Review Letters*, 110(24):248106, 2013.

R. Martínez-García, J. M. Calabrese, and C. López. Online games: A novel approach to explore how partial information influences human random searches. *Scientific*

Reports, 7(1):40029, 12 2017. ISSN 20452322. doi: 10.1038/srep40029. URL `http://www.nature.com/articles/srep40029`.

B. Marwick et al. Pleistocene exchange networks as evidence for the evolution of language. 2003.

W. Mason and S. Suri. Conducting behavioral research on Amazon's Mechanical Turk. *Behavior Research Methods*, 44(1):1–23, 3 2012. ISSN 1554351X. doi: 10.3758/s13428-011-0124-6. URL `http://en.wikipedia.org/wiki/The_Turk`.

N. McGuigan. The role of transmission biases in the cultural diffusion of irrelevant actions. *Journal of Comparative Psychology*, 126(2):150, 2012.

K. Mehlhorn, B. R. Newell, P. M. Todd, M. D. Lee, K. Morgan, V. A. Braithwaite, D. Hausmann, K. Fiedler, and C. Gonzalez. Unpacking the exploration–exploitation tradeoff: A synthesis of human and animal literatures. *Decision*, 2(3):191, 2015.

A. B. Migliano, A. E. Page, J. Gómez-Gardeñes, G. D. Salali, S. Viguier, M. Dyble, J. Thompson, N. Chaudhary, D. Smith, J. Strods, R. MacE, M. G. Thomas, V. Latora, and L. Vinicius. Characterization of hunter-gatherer networks and implications for cumulative culture. *Nature Human Behaviour*, 1(2):1–6, 2017. ISSN 23973374. doi: 10.1038/s41562-016-0043. URL `http://dx.doi.org/10.1038/s41562-016-0043`.

A. B. Migliano, F. Battiston, S. Viguier, A. E. Page, M. Dyble, R. Schlaepfer, D. Smith, L. Astete, M. Ngales, J. Gomez-Gardenes, et al. Hunter-gatherer multilevel sociality accelerates cumulative cultural evolution. *Science Advances*, 6(9): eaax5913, 2020.

A. E. Minetti, C. Moia, G. S. Roi, D. Susta, and G. Ferretti. Energy cost of walking and running at extreme uphill and downhill slopes. *Journal of Applied Physiology*, 93(3):1039–1046, 2002. ISSN 87507587. doi: 10.1152/japplphysiol.01177.2001. URL `http://www.ncbi.nlm.nih.gov/pubmed/12183501http://www.physiology.org/doi/10.1152/japplphysiol.01177.2001`.

O. Miramontes, D. Boyer, and F. Bartumeus. The effects of spatially heterogeneous prey distributions on detection patterns in foraging seabirds. *PloS one*, 7(4):e34317, 2012.

D. Mobbs, P. C. Trimmer, D. T. Blumstein, and P. Dayan. Foraging for foundations in decision neuroscience: Insights from ethology. Technical Report 7, 2018. URL `www.nature.com/nrn`.

U. Mugan and M. A. MacIver. Spatial planning with long visual range benefits escape from visual predators in complex naturalistic environments. *Nature Communications*, 11(1):1–14, 12 2020. ISSN 20411723. doi: 10.1038/s41467-020-16102-1. URL `https://doi.org/10.1038/s41467-020-16102-1`.

M. Muthukrishna, B. W. Shulman, V. Vasilescu, and J. Henrich. Sociality influences cultural complexity. *Proceedings of the Royal Society B: Biological Sciences*, 281 (1774):20132511, 2014.

M. Muthukrishna, T. J. H. Morgan, and J. Henrich. The when and who of social learning and conformist transmission . 2016. doi: 10.1016/j.evolhumbehav.2015.05.004. URL `http://dx.doi.org/10.1016/j.evolhumbehav.2015.05.004`.

V. M. K. Namboodiri, J. M. Levy, S. Mihalas, D. W. Sims, and M. G. Shuler. Rationalizing spatial exploration patterns of wild animals and humans through a temporal discounting framework. *Proceedings of the National Academy of Sciences of the United States of America*, 113(31):8747–8752, 8 2016. ISSN 10916490. doi: 10.1073/pnas.1601664113. URL `https://www.pnas.org/content/113/31/8747?ijkey=55bfcaf8dc6b82403ede835d184fa3cc7d6da73e&keytype2=tf_ipsecsha`.

R. Nathan, W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. A movement ecology paradigm for unifying organismal movement research, 12 2008. ISSN 00278424. URL `http://www.ncbi.nlm.nih.gov/pubmed/19060196http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC2614714`.

V. Nityananda and L. Chittka. Modality-specific attention in foraging bumblebees. *Royal Society Open Science*, 2(10), 2015. ISSN 20545703. doi: 10.1098/rsos.150324.

M. A. Nowak and K. Sigmund. Evolutionary dynamics of biological games. *science*, 303(5659):793–799, 2004.

S. G. Nurzaman, Y. Matsumoto, Y. Nakamura, K. Shirai, S. Koizumi, and H. Ishiguro. An adaptive switching behavior between levy and brownian random search in a mobile robot based on biological fluctuation. In *IEEE/RSJ 2010 International Conference on Intelligent Robots and Systems, IROS 2010 - Conference Proceedings*, pages 1927–1934. IEEE, 10 2010. ISBN 9781424466757. doi: 10.1109/IROS.2010.5651671. URL `http://ieeexplore.ieee.org/document/5651671/`.

D. J. P. O'Sullivan, G. J. O'Keeffe, P. G. Fennell, and J. P. Gleeson. Mathematical modeling of complex contagion on clustered networks. *Frontiers in Physics*, 2015. ISSN 2296-424X. doi: 10.3389/fphy.2015.00071.

L. Pacheco-Cobos, B. Winterhalder, C. Cuatianquiz-Lima, M. F. Rosetti, R. Hudson, and C. T. Ross. Nahua mushroom gatherers use area-restricted search strategies that conform to marginal value theorem predictions. *Proceedings of the National Academy of Sciences of the United States of America*, 116(21):10339–10347, 2019. ISSN 10916490. doi: 10.1073/pnas.1814476116.

S. C. Patrick, D. Pinaud, and H. Weimerskirch. Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *Journal of Animal Ecology*, 86(5):1257–1268, 2017.

E. Pearce. Modelling mechanisms of social network maintenance in hunter–gatherers. *Journal of archaeological science*, 50:403–413, 2014.

C. Perreault and P. J. Brantingham. Mobility-driven cultural transmission along the forager-collector continuum. *Journal of Anthropological Archaeology*, 30(1): 62–68, mar 2011. ISSN 02784165. doi: 10.1016/j.jaa.2010.10.003. URL `https://www.sciencedirect.com/science/article/pii/S0278416510000504`.

N. Pinter-Wollman, R. Wollman, A. Guetz, S. Holmes, and D. M. Gordon. The effect of individual variation on the structure and function of interaction networks in harvester ants. *Journal of the Royal Society Interface*, 8(64):1562–1573, 11 2011. ISSN 17425662. doi: 10.1098/rsif.2011.0059.

D. J. Povinelli and T. J. Povinelli. The Chimpanzees of the Tai Forest: Behavioral Ecology and Evolution. *Ethology*, 2001. ISSN 0179-1613. doi: 10.1046/j.1439-0310.2001.00683.x.

A. Powell, S. Shennan, and M. G. Thomas. Late pleistocene demography and the appearance of modern human behavior. *Science*, 2009. ISSN 00368075. doi: 10.1126/science.1170165.

H. Pöysä. Group foraging in patchy environments: the importance of coarse-level local enhancement. *Ornis scandinavica*, pages 159–166, 1992.

L. S. Premo. Mobility and cultural diversity in central-place Foragers: Implications for the emergence of modern human behavior. In *Learning Strategies and Cultural Evolution During the Palaeolithic*. 2015. ISBN 9784431553632. doi: 10.1007/978-4-431-55363-2_5.

B. A. Purcell and R. Kiani. Hierarchical decision processes that operate over distinct timescales underlie choice and changes in strategy. *Proceedings of the National Academy of Sciences of the United States of America*, 113(31):E4531–E4540, 8 2016. ISSN 10916490. doi: 10.1073/pnas.1524685113.

G. H. Pyke. *Animal movements - an optimal foraging theory approach*, volume 2. Elsevier, second edi edition, 2019. ISBN 9780128132517. doi: 10.1016/B978-0-12-809633-8.90160-2. URL `http://dx.doi.org/10.1016/B978-0-12-809633-8.90160-2`.

M. Rafacz and J. J. Templeton. Environmental Unpredictability and the Value of Social Information for Foraging Starlings. *Ethology*, 109(12):951–960, 12 2003. ISSN 01791613. doi: 10.1046/j.0179-1613.2003.00935.x. URL `http://doi.wiley.com/10.1046/j.0179-1613.2003.00935.x`.

D. A. Raichien, B. M. Wood, A. D. Gordon, A. Z. Mabuiia, F. W. Marlowe, and H. Pontzer. Evidence of Lévy walk foraging patterns inhuman hunter-gatherers. *Proceedings of the National Academy of Sciences of the United States of America*, 111(2):728–733, jan 2014. ISSN 00278424. doi: 10.1073/pnas.1318616111. URL `http://www.ncbi.nlm.nih.gov/pubmed/24367098http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC3896191`.

G. Ramos-Fernández, J. L. Mateos, O. Miramontes, G. Cocho, H. Larralde, and B. Ayala-Orozco. Lévy walk patterns in the foraging movements of spider monkeys (Ateles geoffroyi). *Behavioral Ecology and Sociobiology*, 55(3):223–230, 2004. ISSN 03405443. doi: 10.1007/s00265-003-0700-6. URL `https://link.springer.com/content/pdf/10.1007%2Fs00265-003-0700-6.pdf`.

G. Ramos-Fernández, D. Boyer, and V. P. Gómez. A complex social structure with fission-fusion properties can emerge from a simple foraging model. *Behavioral Ecology and Sociobiology*, 60(4):536–549, aug 2006. ISSN 03405443. doi: 10.1007/s00265-006-0197-x. URL `http://link.springer.com/10.1007/s00265-006-0197-x`.

L. G. Rapaport and G. R. Brown. Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 17(4):189–201, 2008.

E. P. Raposo, S. V. Buldyrev, M. G. da Luz, M. C. Santos, H. E. Stanley, and G. M. Viswanathan. Dynamical robustness of lévy search strategies. *Physical Review Letters*, 91(24), 2003. ISSN 10797114. doi: 10.1103/PhysRevLett.91.240601.

D. Read. an Interaction Model for Resource Implement. 73(4):599–625, 2008.

S. M. Reader. Causes of individual differences in animal exploration and search. *Topics in cognitive science*, 7(3):451–468, 2015.

D. Réale, S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. Integrating animal temperament within ecology and evolution. *Biological reviews*, 82(2):291–318, 2007.

F. Reali, N. Chater, and M. H. Christiansen. Simpler grammar, larger vocabulary: How population size affects language. *Proceedings of the Royal Society B: Biological Sciences*, 2018. ISSN 14712954. doi: 10.1098/rspb.2017.2586.

L. Rendell, R. Boyd, D. Cownden, M. Enquist, K. Eriksson, M. W. Feldman, L. Fogarty, S. Ghirlanda, T. Lillicrap, and K. N. Laland. Why copy others? insights from the social learning strategies tournament. *Science*, 328(5975):208–213, 4 2010. ISSN 00368075. doi: 10.1126/science.1184719. URL `/pmc/articles/PMC2989663//pmc/articles/PMC2989663/?report=abstracthttps://www.ncbi.nlm.nih.gov/pmc/articles/PMC2989663/`.

A. Reynolds. Liberating Lévy walk research from the shackles of optimal foraging, 2015. ISSN 15710645.

A. Reynolds, E. Ceccon, C. Baldauf, T. K. Medeiros, and O. Miramontes. Lévy foraging patterns of rural humans. *PLoS ONE*, 13(6):e0199099, jun 2018. ISSN 19326203. doi: 10.1371/journal.pone.0199099. URL `https://dx.plos.org/10.1371/journal.pone.0199099`.

A. M. Reynolds. Optimal random Lévy-loop searching: New insights into the searching behaviours of central-place foragers. *Epl*, 82(2):20001, 4 2008. ISSN 02955075. doi: 10.1209/0295-5075/82/20001. URL `http://stacks.iop.org/0295-5075/82/i=2/a=20001?key=crossref.edd55ca8f1a6ae994b439e0ba23a810a`.

A. M. Reynolds and M. A. Frye. Free-flight odor tracking in Drosophila is consistent with an optimal intermittent scale-free search. *PLoS ONE*, 2(4):e354, 4 2007. ISSN 19326203. doi: 10.1371/journal.pone.0000354. URL `http://www.ncbi.nlm.nih.gov/pubmed/17406678http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC1831497`.

A. M. Reynolds, Y. Ropert-Coudert, A. Kato, A. Chiaradia, and A. J. MacIntosh. A priority-based queuing process explanation for scale-free foraging behaviours.

Animal Behaviour, 108:67–71, 10 2015. ISSN 00033472. doi: 10.1016/j.anbehav.2015.07.022.

T. Rhodes, C. T. Kello, and B. Kerster. Intrinsic and extrinsic contributions to heavy tails in visual foraging. *Visual Cognition*, 22(6):809–842, 7 2014. ISSN 14640716. doi: 10.1080/13506285.2014.918070. URL `http://www.tandfonline.com/doi/abs/10.1080/13506285.2014.918070`.

G. Rieucau and L.-A. Giraldeau. Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567):949–957, 2011.

H. Rita, E. Ranta, and N. Peuhkuri. Group foraging, patch exploitation time and the finder's advantage. *Behavioral Ecology and Sociobiology*, 40(1):35–39, 1997.

A. R. Rogers. Does biology constrain culture? *American Anthropologist*, 90(4): 819–831, 1988.

V. Romano, S. Lozano, and J. Fernández-López de Pablo. A multilevel analytical framework for studying cultural evolution in prehistoric hunter–gatherer societies. *Biological Reviews*, 2020. ISSN 1469185X. doi: 10.1111/brv.12599.

A. G. Rosati. Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, 21(9):691–702, 2017. ISSN 1879307X. doi: 10.1016/j.tics.2017.05.011. URL `http://dx.doi.org/10.1016/j.tics.2017.05.011`.

C. T. Ross and B. Winterhalder. Sit-and-wait versus active-search hunting: A behavioral ecological model of optimal search mode. *Journal of Theoretical Biology*, 387:76–87, 2015. ISSN 10958541. doi: 10.1016/j.jtbi.2015.09.022. URL `http://dx.doi.org/10.1016/j.jtbi.2015.09.022`.

J. Ross, L. Irani, M. S. Silberman, A. Zaldivar, and B. Tomlinson. Who are the crowdworkers? Shifting demographics in mechanical turk. In *Conference on Human Factors in Computing Systems - Proceedings*, pages 2863–2872, New York, New York, USA, 2010. ACM Press. ISBN 9781605589312. doi: 10.1145/1753846.1753873. URL `http://portal.acm.org/citation.cfm?doid=1753846.1753873`.

T. Sakiyama and Y. P. Gunji. Emergent weak home-range behaviour without spatial memory. *Royal Society Open Science*, 3(6), 2016. ISSN 20545703. doi: 10.1098/rsos.160214. URL `http://dx.doi.org/10.1098/rsos.160214orviahttp://rsos.royalsocietypublishing.org`.

L. C. Salvador, F. Bartumeus, S. A. Levin, and W. S. Ryu. Mechanistic analysis of the search behaviour of Caenorhabditis elegans. *Journal of the Royal Society Interface*, 11(92), 2014. ISSN 17425662. doi: 10.1098/rsif.2013.1092. URL `http://rsif.royalsocietypublishing.org`.

E. Schulz, C. M. Wu, Q. J. Huys, A. Krause, and M. Speekenbrink. Generalization and Search in Risky Environments. *Cognitive Science*, 42(8):2592–2620, 2018. ISSN 15516709. doi: 10.1111/cogs.12695.

T. D. Seeley and S. C. Buhrman. Group decision making in swarms of honey bees. *Behavioral Ecology and Sociobiology*, 45(1):19–31, 1 1999. ISSN 03405443. doi: 10.1007/s002650050536. URL `http://link.springer.com/10.1007/s002650050536`.

J.-T. Seppänen, J. T. Forsman, M. Mönkkönen, and R. L. Thomson. Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, 88(7):1622–1633, 2007.

L. Seuront and H. E. Stanley. Anomalous diffusion and multifractality enhance mating encounters in the ocean. *Proceedings of the National Academy of Sciences of the United States of America*, 111(6):2206–2211, 2 2014. ISSN 00278424. doi: 10.1073/pnas.1322363111. URL `http://www.ncbi.nlm.nih.gov/pubmed/24469823http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC3926071`.

M. F. Shlesinger. Mathematical physics: Search research. *Nature*, 443(7109):281–282, 9 2006. ISSN 14764687. doi: 10.1038/443281a. URL `http://www.nature.com/articles/443281a`.

M. Shott. Technological organization and settlement mobility: an ethnographic examination. *Journal of Anthropological Research*, 42(1):15–51, 1986.

M. Sikora, A. Seguin-Orlando, V. C. Sousa, A. Albrechtsen, T. Korneliussen, A. Ko, S. Rasmussen, I. Dupanloup, P. R. Nigst, M. D. Bosch, et al. Ancient genomes show social and reproductive behavior of early upper paleolithic foragers. *Science*, 358(6363):659–662, 2017.

H. A. Simon. Rational choice and the structure of the environment. *Psychological review*, 63(2):129, 1956.

D. W. Sims, E. J. Southall, N. E. Humphries, G. C. Hays, C. J. Bradshaw, J. W. Pitchford, A. James, M. Z. Ahmed, A. S. Brierley, M. A. Hindell, D. Morritt, M. K. Musyl, D. Righton, E. L. Shepard, V. J. Wearmouth, R. P. Wilson, M. J. Witt, and J. D. Metcalfe. Scaling laws of marine predator search behaviour. *Nature*, 451(7182):1098–1102, 2 2008. ISSN 14764687. doi: 10.1038/nature06518. URL `http://www.nature.com/articles/nature06518`.

D. W. Sims, N. E. Humphries, N. Hu, V. Medan, and J. Berni. Optimal searching behaviour generated intrinsically by the central pattern generator for locomotion. *eLife*, 8:1–31, 2019. ISSN 2050084X. doi: 10.7554/eLife.50316. URL `https://elifesciences.org/articles/50316`.

S. J. Sloman, R. L. Goldstone, and C. Gonzalez. A social interpolation model of group problem-solving. *Cognitive Science*, 45(12):e13066, 2021.

P. E. Smaldino. Models are stupid, and we need more of them. In *R Vallacher, SJ Read, & A Nowak (Eds.), Computational Social Psychology*, pages 311–331. Psychology Press, New York, 2017.

P. E. Smaldino and J. C. Schank. Movement patterns, social dynamics, and the evolution of cooperation. *Theoretical population biology*, 82(1):48–58, 2012.

M. Smolla and E. Akçay. Cultural selection shapes network structure. *Science advances*, 5(8):eaaw0609, 2019.

M. Smolla, R. Tucker Gilman, T. Galla, and S. Shultz. Competition for resources can explain patterns of social and individual learning in nature. *Proceedings of the Royal Society B: Biological Sciences*, 282(1815), 2015. ISSN 14712954. doi: 10.1098/rspb.2015.1405. URL `https://pubmed.ncbi.nlm.nih.gov/26354936/`.

J. Spaethe, J. Tautz, and L. Chittka. Do honeybees detect colour targets using serial or parallel visual search? *Journal of Experimental Biology*, 209(6):987–993, 7 2006. ISSN 00220949. doi: 10.1242/jeb.02124.

W. D. Spencer. Home ranges and the value of spatial information. *Journal of Mammalogy*, 93(4):929–947, sep 2012. ISSN 0022-2372. doi: 10.1644/12-mamm-s-061.1. URL `https://academic.oup.com/jmammal/article-lookup/doi/10.1644/12-MAMM-S-061.1`.

D. W. Stephens. Decision ecology: Foraging and the ecology of animal decision making. *Cognitive, Affective and Behavioral Neuroscience*, 8(4):475–484, 2008. ISSN 15307026. doi: 10.3758/CABN.8.4.475.

J. Steward. Cultural ecology. *International Encyclopedia of the Social Sciences*, 4: 337–344, 1968.

S. S. Strassberg and N. Creanza. Cultural evolution and prehistoric demography. *Philosophical Transactions of the Royal Society B*, 376(1816):20190713, 2021.

W. Toyokawa, A. Whalen, and K. N. Laland. Social learning strategies regulate the wisdom and madness of interactive crowds. *Nature Human Behaviour*, 3(2):183–193, 2 2019. ISSN 23973374. doi: 10.1038/s41562-018-0518-x. URL `www.nature.com/nathumbehav`.

A. Vazquez. Impact of memory on human dynamics. *Physica A: Statistical Mechanics and its Applications*, 373:747–752, 2007. ISSN 03784371. doi: 10.1016/j.physa.2006.04.060.

V. V. Venkataraman, T. S. Kraft, N. J. Dominy, and K. M. Endicott. Hunter-gatherer residential mobility and the marginal value of rainforest patches. *Proceedings of* *the National Academy of Sciences of the United States of America*, 2017. ISSN 10916490. doi: 10.1073/pnas.1617542114.

W. L. Vickery, L.-A. Giraldeau, J. J. Templeton, D. L. Kramer, and C. A. Chapman. Producers, scroungers, and group foraging. *The american naturalist*, 137(6):847–863, 1991.

W. F. Vining, F. Esponda, M. E. Moses, and S. Forrest. How does mobility help distributed systems compute? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2019. ISSN 14712970. doi: 10.1098/rstb.2018.0375.

G. M. Viswanathan, V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. Levy flight search patterns of wandering albatrosses. *Nature*, 381 (6581):413–415, 5 1996. ISSN 0028-0836. doi: 10.1038/381413a0. URL `http://www.nature.com/doifinder/10.1038/381413a0`.

G. M. Viswanathan, S. V. Buldyrev, S. Havlin, M. G. Da Luz, E. P. Raposo, and H. E. Stanley. Optimizing the success of random searches. *Nature*, 401(6756): 911–914, 1999. ISSN 00280836. doi: 10.1038/44831.

G. M. Viswanathan, M. G. Da Luz, E. P. Raposo, and H. E. Stanley. *The physics of foraging: An introduction to random searches and biological encounters*, volume 9781107006. Cambridge University Press, Cambridge, 2011. ISBN 9780511902680. doi: 10.1017/CBO9780511902680. URL `http://ebooks.cambridge.org/ref/id/CBO9780511902680`.

K. Von Frisch. *The dance language and orientation of bees*. Harvard University Press, 2013.

A. Ward and M. Webster. Social foraging and predator-prey interactions. In *Sociality: The Behaviour of Group-Living Animals*, pages 55–87. Springer, 2016.

A. J. Ward, P. Thomas, P. J. Hart, and J. Krause. Correlates of boldness in three-spined sticklebacks (gasterosteus aculeatus). *Behavioral Ecology and Sociobiology*, 55(6):561–568, 2004.

V. J. Wearmouth, M. J. Mchugh, N. E. Humphries, A. Naegelen, M. Z. Ahmed, E. J. Southall, A. M. Reynolds, and D. W. Sims. Scaling laws of ambush predator 'waiting' behaviour are tuned to a common ecology. *Proceedings of the Royal Society B: Biological Sciences*, 281(1782), 3 2014. ISSN 14712954. doi: 10.1098/rspb.2013.2997.

M. Webster and K. Laland. Social information, conformity and the opportunity costs paid by foraging fish. *Behavioral Ecology and Sociobiology*, 66(5):797–809, 2012.

R. Whallon. Social networks and information: Non-"utilitarian" mobility among hunter-gatherers. *Journal of Anthropological Archaeology*, 2006. ISSN 02784165. doi: 10.1016/j.jaa.2005.11.004.

A. Whiten and D. Erdal. The human socio-cognitive niche and its evolutionary origins. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367 (1599):2119–2129, 2012.

C. Wiesner, V. V. Vliet, E. Butt, H. Pavensta, M. Sto, S. Linder, and J. Kremerskothen. Lasp-1 Regulates Podosome Function. *PloS one*, 7(4):1–10, 2012. ISSN 00113891. doi: 10.1371/Citation.

P. Wiessner. Hunting, healing, and hxaro exchange. A long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evolution and Human Behavior*, 2002. ISSN 10905138. doi: 10.1016/S1090-5138(02)00096-X.

A. Wilke and H. C. Barrett. The hot hand phenomenon as a cognitive adaptation to clumped resources. *Evolution and Human Behavior*, 30(3):161–169, 5 2009. ISSN 10905138. doi: 10.1016/j.evolhumbehav.2008.11.004.

R. P. Wilson, F. Quintana, and V. J. Hobson. Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B: Biological Sciences*, 279(1730):975–980, 3 2012. ISSN 14712970. doi: 10.1098/rspb.2011.1544. URL `www.fishbase.orghttp://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2011.1544`.

B. Winterhalder. Hominid paleoecology and competitive exclusion: Limits to similarity, niche differentiation, and the effects of cultural behavior. *American Journal of Physical Anthropology*, 1981. ISSN 10968644. doi: 10.1002/ajpa.1330240505.

B. Winterhalder. Diet choice, risk, and food sharing in a stochastic environment. *Journal of anthropological archaeology*, 5(4):369–392, 1986.

B. Winterhalder. Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 5(2):46–57, 1996.

H. M. Wobst. Boundary conditions for paleolithic social systems: a simulation approach. *American Antiquity*, 39(2Part1):147–178, 1974.

R. C. Ydenberg, C. V. Welham, R. Schmid-hempel, P. Schmid-hempel, and G. Beauchamp. Time and energy constraints and the relationships between currencies in foraging theory. Technical Report 1, 1994.

M. Zhang, J. Feng, K. T. Ma, J. H. Lim, Q. Zhao, and G. Kreiman. Finding any Waldo with zero-shot invariant and efficient visual search. *Nature Communications*, 9(1):1–15, 12 2018. ISSN 20411723. doi: 10.1038/s41467-018-06217-x. URL `www.nature.com/naturecommunications`.

P. A. Zollner and S. L. Lima. Search Strategies for Landscape-Level Interpatch Movements. Technical Report 3, 1999.

D. Zurick, Valli, R. Farkas, and H. Troyer. *Land of pure vision: The sacred geography of Tibet and the Himalaya*. University Press of Kentucky, 2014. ISBN 9780813145594.