

**The Interplay between Resource Distributions and Optimal Foraging
Behavior: From Individuals to Populations**

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List of Acronyms

OFT	optimal foraging theory
MSD	mean squared displacement
pdf	probability density function
GMM	Gaussian mixture model
SLLVM	stochastic lattice Lotka-Volterra model
NLM	neutral landscape model

Samenvatting

– Summary in Dutch –

Foerageren beschrijft het zoeken naar hulpbronnen, zoals voedsel of een schuilplaats, en is voor veel diersoorten essentieel om te overleven. Daarom wordt verwacht dat foerageerders hun gedrag aanpassen om zo hun overlevingskansen te maximaliseren. Aangezien foerageren alomverteenwoordigd is in de natuur, denkt men dat voordelen tijdens foerageren grote evolutionaire druk uitoefenen op diersoorten, en mogelijk zelfs ten grondslag liggen aan het ontstaan van ingewikkelde zoekstrategieën, complex sociaal gedrag, en indrukwekkende cognitieve vaardigheden zoals geheugen. Recente ontwikkelingen zijn pas net begonnen met het onttrafen van de complexe mechanismen achter optimaal foerageergedrag, en vele vragen blijven vooralsnog onbeantwoord.

Specifiek foerageergedrag hangt sterk af van het *doel* van het dier, ofwel, waar is de foerageerder naar op zoek? In zogeheten ‘optimale foerageertheorie’, wordt aangenomen dat foerageerders gedrag vertonen dat resulteert in het maximaliseren van een specifieke metriek, vaak de *valuta* genoemd. Een veel gebruikte valuta is het aantal bronnen dat wordt verzameld binnen een bepaalde tijd: de foerageerefficiëntie. Deze metriek kan echter niet al het foerageer gedrag dat wordt waargenomen in de natuur verklaren. De reden hiervoor is dat foerageerders vaak bijkomende doeleinden nastreven, zoals individuele overleving of het voortbestaan van de soort. Hoogstwaarschijnlijk zijn er andere, misschien tot nog toe onontdekte, doelen die evolutionaire druk uitoefenen op foerageerders om hun gedrag aan te blijven passen.

Welk foerageergedrag optimaal is, hangt vaak sterk samen met verschillende factoren. Daarom richten we ons in dit proefschrift op de wisselwerking van verschillende doelen en dergelijke factoren, en bestuderen we hoe verschillende factoren de voordelen van specifiek foerageergedrag bepalen. Een van de belangrijkste factoren is de configuratie van hun leefgebieden, of, met andere woorden, de verdeling van hulpbronnen. Daarom onderzoeken we specifiek hoe foerageergedrag wordt beïnvloed door deze verdeling en hoe specifieke omgevingseigenschappen de individuen in staat stellen om deze in hun voordeel te gebruiken. Bovendien toont het werk in dit proefschrift aan dat foerageerders zelf ook de verdeling over hulpbronnen kunnen beïnvloeden. Als gevolg oefenen foerageer-

ders een sterke invloed uit op de onderliggende structuur van de gebieden waarin ze leven.

Onderliggend aan bijna elk optimaal foerageergedrag ligt een efficiënte zoekstrategie. Aangezien de locatie van hulpbronnen initiëel vaak onbekend zijn voor de foerageerder, wordt een groot deel van de optimale foerageertheorie gewijd aan hoe willekeurige zoekacties kunnen worden geoptimaliseerd. Terwijl deze zoekacties, zoals hun naam suggereert, inherent willekeurig zijn, kunnen ze interessant genoeg nog steeds effectief worden gebruikt. In het bijzonder bestaat een bepaald type willekeurige beweging die zogeheten 'schaalvrije' kenmerken vertoont; *Lévy walks*. Lévy walks, of Lévy searches, omvatten een breed scala aan bewegingen en beschrijven willekeurig zoekgedrag waarin lokaal zoekgedrag wordt afgewisseld met zeldzame, maar statistisch relevante, verplaatsingen over lange afstanden. Met andere woorden, Lévy walks wisselen af tussen het intensief zoeken van een klein gebied, om alvorens te 'springen' naar een verafgelegen gebied dat mogelijks van belang is.

In het algemeen vertonen de meeste leefgebieden zogeheten *heterogeniteit*, omdat bronnen in de natuur de neiging hebben om in clusters voor te komen. Dit soort heterogene omgevingen zijn bovendien van belang omdat veel ecosystemen in omvang verminderen, vaak als gevolg van menselijke invloeden. Door vermindering van geschikt habitat worden gebieden vaak opgedeeld in kleinere gebieden, waardoor afzonderlijke stukken natuur steeds meer geïsoleerd raken. Dit proces heet fragmentatie, en heeft vaak negatieve effecten op dierpopulaties in natuurgebieden. Daarom is het van cruciaal belang om foerageergedrag in dit soort heterogene gebieden beter te begrijpen. In dit proefschrift worden verschillende foerageerstrategieën besproken en deze zullen allemaal in heterogene gebieden worden onderzocht. Het doel van dit proefschrift is om meer te leren over de ingewikkelde wisselwerking tussen foerageerders en de gebiedend waarin ze leven.

Ten eerste beschouwen we een systeem van een enkele foerageerder die het vermogen heeft om een ruimtelijke verdeling te leren. Zo een geheugencomponent kan worden gebruikt door de foerageerder om naar plekken, waarvan wordt verwacht dat ze rijk aan hulpbronnen zijn, te gaan. We beargumenteren welke eigenschappen een geheugencomponent nodig heeft en zullen de mogelijke voordelen voor de foerageerder uitlichten. Iets specifieker, we onderzoeken een hybride strategie die exploratie, met een Lévy walk, afwisselt met exploitatie, met geïnformeerde verplaatsingen door gebruik te maken van geheugen. Daarna bekijken we hoe het optimale foerageergedrag wordt beïnvloed door twee verschillende doelen: de foerageerefficiëntie en de brondiversiteit. De eerste term komt overeen met de definitie hierboven, d.w.z. de hoeveelheid bronnen per tijds-eenheid, terwijl de laatste term daarbovenop beschouwt uit welk gebied de bronnen afkomstig zijn en dus rekening houdt met mogelijks verschillende hulpbronnen. Onze resultaten tonen aan dat foerageerders voordeel

halen uit het gebruik van geheugen door voortdurend een beperkte aantal bronrijke plekken te bezoeken, waarvan de locaties effectief in het geheugen zijn opgeslagen. Dit beperkt de foerageerder echter wel tot het bezoeken van een beperkt gebied, en de brondiversiteit neemt als gevolg hierdoor dan ook af. Aangezien de meeste foerageerders vaak een variatie aan hulpbronnen nodig hebben om te overleven, bijvoorbeeld zowel voedsel als water, suggereert dit resultaat dat foerageergedrag dat gebaseerd is op geheugen niet per se gunstig is. Onze resultaten ondersteunen de hypothese dat foerageergedrag sterk moet afhangen van het specifieke doel van de foerageerder.

Ten tweede, aangezien foerageerders niet altijd solitair zijn, bestuderen we een groep foerageerders en bekijken we hoe hun gedrag wordt beïnvloed door de clustereigenschappen van hulpbronnen. We beschouwen foerageerders die de karakteristieken van hun Lévy walk kunnen veranderen wanneer ze hulpbronnen tegenkomen, door over te schakelen naar een meer intensieve, gelokaliseerde zoekstrategie. We bestuderen een systeem waar het zoekgedrag van soortgenoten kan worden opgemerkt en waar foerageerders bewegen richting degenen die intensief zoeken, omdat dit een indicatie is dat zich daar een cluster met meerdere hulpbronnen bevindt. Het is belangrijk om te beseffen dan, omdat het aantal hulpbronnen in de clusters beperkt is, de foerageerders concurrenten van elkaar zijn. Door precies de clustereigenschappen van de bronverdelingen te controleren, kunnen we kwantitatief de voordelen van foerageren in groepen bepalen. We bestuderen twee doeleinden: de efficiëntie van de groep en de overlevingskans van individuen. Onze resultaten tonen aan dat aggregaties op de clusters alleen voordelig zijn voor de groep als de bronnen sterk geclusterd zijn, omdat dit de concurrentie op de clusters tot een minimum beperkt. Foerageren in groepen blijkt nadelig wanneer concurrentie toeneemt, wat gebeurt wanneer de bronnen niet sterk geclusterd zijn of wanneer er simpelweg heel veel foerageerders zijn. Dit staat in schril contrast met individuele overlevingskansen, die gemaximaliseerd worden juist wanneer de bronnen niet sterk geclusterd zijn. We meten hier de overlevingskans als de afwijking van het gemiddelde, en laten zien dat deze afwijking het laagst is wanneer het groepsgemiddelde laag is. Daarom komen de resultaten van ons model overeen met de realiteit, waar vaak wordt waargenomen dat foerageerders niet per se de foerageerefficiëntie optimaliseren, maar dat ze, wanneer mogelijk, de variatie in het aantal gevonden hulpbronnen willen verminderen om zo hun overlevingskansen te vergroten.

Ten derde onderzoeken we een collectief systeem waarin foerageerders kunnen samenwerken, in plaats van te concurreren. Daartoe introduceren we een model waarin foerageerders andere foerageerders kunnen rekruteren naar bronlocaties, in plaats van zelf de hulpbron te exploiteren (bijvoorbeeld door voedsel te consumeren). Rekrutering zelf betreft ook een willekeurige zoektocht, een Lévy walk, maar dan voor soortgenoten

en niet voor hulpbronnen. We laten zien dat deze zoektochten geoptimaliseerd kunnen worden onder redelijke aannames. Verder bestuderen we clusters van hulpbronnen die slechts voor een beperkte tijd beschikbaar zijn. In zulke situaties is rekrutering alleen gunstig voor het collectief als soortgenoten snel gevonden kunnen worden, zodat deze tijdig de hulpbron kunnen exploiteren. Daarom beargumenteren we dat foerageerders geen soortgenoten moeten proberen te rekruteren naar clusters die korter bestaan dan een bepaalde duur; de tijdsdrempel. We bestuderen hoe de effectiviteit van deze eenvoudige collectieve strategie afhangt van de gemiddelde tijdsduur van bronnen. Onze resultaten geven aan dat rekrutering alleen gunstig is voor het collectief als de clusters met bronnen moeilijk te vinden zijn en een relatief lange tijdsduur hebben. Bovendien wordt de collectieve foerageerefficiëntie positief beïnvloedt door een verhoogd aantal interacties met soortgenoten, wat gebeurt bij hogere effectieve dichtheden van soortgenoten. Verder suggereren onze resultaten dat de specifieke waarde van de tijdsdrempel een eerder beperkte invloed heeft, terwijl de keuze om te rekruteren of niet van kritiek belang is. Dit resultaat kan verstrekkende gevolgen hebben voor toekomstige toepassingen in artificiële foerageersystemen, omdat ons model aangeeft dat complexe beslissingen, die mogelijk hoge cognitieve capaciteiten vereisen, niet nodig zijn om te kunnen profiteren van collectief gedrag.

Ten vierde onderzoeken we hoe de fragmentatie van landschappen en foerageergedrag de dynamiek van populaties beïnvloeden. Daartoe transformeren we ons foerageer-hulpbron systeem, zonder demografische gebeurtenissen zoals sterfte, naar een roofdier-prooi systeem dat dergelijke gebeurtenissen wel bevat. We beschouwen prooien die zich niet ver kunnen verplaatsen en, als gevolg van fragmentatie, daarom alleen in de afzonderlijke geïsoleerde fragmenten kunnen overleven. Roofdieren kunnen wel tussen de fragmenten bewegen, waarbij we hun verplaatsing zorgvuldig controleren d.m.v. een Lévy walk. Door het variëren van het fragmentatieniveau onderzoeken we de effecten van fragmentatie op populaties van roofdieren en hun prooi. Onze resultaten voorspellen dat de effecten van fragmentatie op populaties meestal negatief zijn, maar het daadwerkelijke effect hangt sterk af van hoe de roofdieren zich bewegen tussen de geïsoleerde gebieden. Onze resultaten tonen aan dat de optimale bewegingspatronen van roofdieren gekenmerkt worden door een hoge dispersiegraad, om zowel verafgelegen gebieden te bezoeken én deze bij aankomst niet teveel te exploiteren. Wanneer fragmentatie toeneemt, neemt deze optimale dispersiegraad ook toe, maar totale populatiegroottes nemen sterk af. Omdat prooi verhinderd is om zich naar andere fragmenten te verplaatsen, zorgt fragmentatie er voor dat lokale prooipopulaties zeer gevoelig zijn voor demografische fluctuaties, en dus meer kans hebben om (lokaal) uit te sterven door overconsumptie. Onze resultaten laten zien dat kleine fragmenten veel gevoeliger zijn aan deze schommelingen en dus meer kans hebben om onomkeerbaar uitgeput te raken. Aange-

zien sterk gefragmenteerde landschappen gemiddeld veel meer kleine gebieden bevatten, wordt onomkeerbaar verlies van habitat in zulke landschappen verergerd. Onze resultaten suggereren echter dat een optimale respons van roofdieren de totale hoeveelheid verloren habitat sterk kan verminderen. Hoewel het verlies niet kan worden voorkomen, laten onze resultaten zien dat foerageergedrag, dat zich uit in de verplaatsingen tussen de geïsoleerde fragmenten, van cruciaal belang is voor de stabiliteit van ecosystemen.

Het gepresenteerde werk in dit proefschrift benadrukt het ingewikkelde samenspel van verschillende factoren op optimaal foerageergedrag. We richten ons specifiek op hoe foerageerders worden beïnvloedt door, en reageren op, veranderingen in ecosystemen en dragen zo bij aan de discussie over hoe optimaal foerageergedrag voortdurend gevormd wordt door cognitieve capaciteiten, interacties met soortgenoten en de onderliggende structuur van het landschap.

Summary

Foraging describes the search for resources essential to the long-term survival of many animal species. Therefore, foragers are expected to optimize their foraging behavior as to maximize their odds of survival. As survival is the primary concern of species, it is unsurprising that foraging is ubiquitous in nature. Moreover, it is believed that foraging advantages, thus increased survival probabilities, exert major evolutionary pressure on species, possibly underlying emergence of intricate search strategies, complex social behavior, and impressive cognitive feats such as memory. Recent developments have only started to unveil the complex decision mechanisms behind optimal foraging behavior and many questions remain still unanswered.

Specific foraging behavior strongly depends on the *incentive* of the forager, i.e. what is the forager looking for? In optimal foraging theory, it is assumed that foragers exhibit behavior that results in maximizing some metric, often called the *currency*. A widely employed currency is the number of resources gathered per unit time: the *foraging efficiency*. However, foraging efficiency alone cannot explain all foraging patterns that have been observed in natural systems, as foragers often address other important incentives, such as *individual survival* or *species persistence*. Most likely, other, perhaps yet undiscovered, incentives pressure foragers into further adapting their behavior.

What foraging behavior is optimal, often heavily depends on several other external factors. Therefore, in this dissertation, we focus on how different foraging incentives are influenced by such factors and how different factors strongly determine advantages of specific foraging behaviors. Among the most important external factor is the spatial configuration of the resource distribution. Therefore, we specifically examine how foraging behavior is influenced by the distribution over resources and how specific distributions enable individuals to take advantage of, for example, memory or conspecifics. Furthermore, the work in this dissertation shows that foragers are not only influenced by resource distributions, but can in turn effectively influence the resource distribution themselves. Consequently, foragers strongly affect the underlying habitat structure of the environments wherein they live.

Regardless of the incentives or factors, underlying nearly all optimal foraging behavior are efficient searches. As the locations of resources are

often *a priori* unknown to the forager, a large part of optimal foraging theory pertains the study of *random searches*. Interestingly, while random searches, or random walks, are, as their name suggests, inherently random, they can still be employed effectively and have been observed to optimize foraging efficiencies over a wide range of resource distributions. In our particular interest is a random walk that expresses scale-free characteristics in forager dispersal; the so-called *Lévy walk*. Lévy walks encompass a wide range of movements and describe random walks that interchange local search behavior with rare, but statistically relevant, long-range displacements. In other words, Lévy walks encode for the search behavior, and thus foraging strategy, of searching a small area intensively before jumping towards a next far-away area of interest.

In general, the environments that shall be discussed exhibit spatial heterogeneity, as resources in natural systems tend to be clustered on patches. Patchy environments are furthermore of interest as many ecosystems are decreasing in size, often due to anthropogenic influences. These reductions in suitable habitat are often accompanied by increased fragmentation, where habitat is broken up into smaller and more isolated patches. For conservation purposes, it is consequently of critical importance to understand how foragers respond to these, mostly negative, changes in spatial resource configurations. The foraging strategies that are discussed in this dissertation, will pertain to optimal foraging behavior in patchy, or fragmented, landscapes. In general, the aim is to highlight and study the intricate interplay between foragers and the environments they inhabit.

To this end, we first consider a system of a single forager that is equipped with the ability to learn a spatial distribution. Such an ability is widely observed in many species and it effectively allows organisms to direct their movement towards patches known to be rich in resources. We discuss what type of memory allows for the recollection of patch locations and discuss potential benefits for foraging. More specifically, we examine how a hybrid foraging strategy, that interchanges exploration, by Lévy walk, and exploitation, by informed displacements, influences optimal foraging behavior for two different incentives: foraging efficiency and patch diversity. The former corresponds to the definition above, i.e. the number of resources per unit time, while the latter additionally considers from what patch the resources originated, thus representing the diversity over consumed resources. Our results reveal that foragers can benefit from spatial memory by continuously exploiting a limited set of resource rich patches of which the locations are effectively stored in memory. However, this restricts forager movement to a limited area and exploration is effectively suppressed. As a result, frequent memory usage is associated with a decline in patch diversity. As foragers often need a diverse set of resources to survive, such as food and water, this suggests that spatial memory is not necessarily always beneficial. Therefore, our results illustrate the idea that foraging behavior should critically depend on the incentive of the forager.

Second, as foragers are not always solitary, we study a group of foragers and how their behavior is affected by resource patchiness. We consider foragers that change the characteristics of their Lévy walk upon entering a patch, by switching from an extensive search with long-displacements, to an intensive, more localized search. We study a system where the search behavior of nearby conspecifics can be monitored and foragers are attracted to those that search intensively, as this signifies patch existence. Because the set of resources on patches was limited, foragers are effectively competing with one another. By controlling resource patchiness, we quantitatively determine the benefits of joining for two incentives: group foraging efficiency and individual survival probability. Our results show that joining others increased the group foraging efficiency only when patches contained sufficient resources, as it effectively keeps competition rates on patches to a minimum. Joining is found to not be beneficial when competition increased, which occurs when resources are not densely clustered or when effective foraging densities are high. Interestingly, individual survival probabilities, that are maximized when the variation in resource intake is minimized, are greatest precisely when group foraging efficiencies are minimized. Therefore, our results conform to empirical observations that, while foraging in groups can be advantageous for the individual under certain environmental conditions, many foragers instead resort to so-called 'low mean, low variance' strategies as to increase the odds of survival.

Third, we examine a collective system wherein foragers exhibit altruistic behavior instead of competition between individuals. To this end, we introduce an agent-based model wherein foragers can recruit other foragers to ephemeral patches instead of exploiting the patch by themselves. Recruitment regards a random search, here a Lévy walk for conspecifics, which we show can be optimized under some reasonable assumptions. As patches only persist for some time, recruitment can only be considered beneficial for the collective if it provided a net gain in resource intake. Therefore, patches with a duration below a certain threshold should not trigger recruitment behavior, while those that persist long enough should. We study how the effectiveness of such threshold-based recruitment behavior depends on resource ephemerality, by controlling the time over which patches persist and examining the collective foraging efficiency as the incentive. Our results indicate that recruitment is only beneficial to the collective if patches (thus resources) are difficult to locate and sufficiently persistent. Additionally, collective foraging efficiencies are positively affected by increased conspecific encounter rates mediated by increases in effective forager densities. Furthermore, our results indicate that the particular value of the recruitment threshold has limited impact, whereas the choice whether to recruit is critical. This result can have profound consequences for future applications in artificial foraging systems, as our model suggests that complex decisions needing high cognitive capabilities are not neces-

sary to benefit from collective behavior.

Fourth, we investigate how landscape fragmentation and optimal foraging behavior jointly influence population dynamics. To this end, we transform our forager-resource system without demographic events, such as birth and death processes, to a predator-prey system that included such events. We consider sessile prey species that, as a result of fragmentation, can inhabit only spatially separated fragments (patches). In contrast, predators can move between the fragments, where their dispersal rates were precisely controlled by having them assume Lévy walks. By varying landscape fragmentation and predator dispersal rates, we closely examine their effects on predator and prey populations. Our results predict that the effects of fragmentation on population densities are mostly negative, however the strength of the effects depend strongly on predator dispersal. More specifically, our results show that optimal predator responses in landscapes that display little fragmentation are to adopt high dispersal rates, as to both visit far away patches while not overexploiting them upon arrival. Increases in fragmentation, in contrast, result in decreases in optimal dispersal rates for population densities to be maximal. As we consider prey to be sessile, fragmentation prevents prey from moving between fragments and, as such, small local prey populations become highly sensitive to demographic fluctuations. Our results indicate that small patches are much more sensitive to these fluctuations and are thus more likely to become irreversibly depleted. As highly fragmented landscapes contain, on average, more smaller patches, irreversible habitat loss is exacerbated in such landscapes. However, our results suggest that optimal predator responses to high degrees of habitat fragmentation can reduce, but not prevent, the amount of lost habitat. These results cement the critical importance of forager dispersal on the stability of ecosystems.

The presented work in this dissertation highlights the intricate interplay of internal and external factors on optimal foraging behavior. We specifically focus on individual-based behavioral responses to environmental influences and thereby contribute towards the discussion on how optimal foraging behavior is continuously shaped by cognitive capabilities, interactions with conspecifics and the structure of the resource landscape.

1

Introduction

1.1 Foraging

Imagine looking for your keys as you are leaving your house, yet you cannot remember the last location where you have seen them. As you are running late, you would like to optimize your search strategy such that the expected time to find your keys is minimized. What kind of strategy would you employ? One might first look in places with a high probability of the key being there, such as a drawer, or a particular spot where the key normally sits. Others may instead try to mentally retrace their activities, in order to recall where they might have left it the day before. Most likely, the more places that you have searched without success, the more exhaustive your search will become. As the key does not move, a search strategy that eliminates likely locations one-by-one, slowly turning into a full exhaustive search if the key remains elusive, is probably the search strategy that many will resort to.

While the above example might come across as a relatively simple task, perhaps one that occurs almost daily to some, the underlying decision process is in fact extremely complex. It combines complex spatial memory with likelihood models of where the key might be, all while smoothly transitioning into different search strategies depending on the time elapsed without finding the key. Now, whereas finding the key is not essential to surviving, one can imagine animals searching for food in very similar ways. The process of looking for essential resources, such as food, a nesting site, or potential mates, of which locations of the resources are often *a priori* unknown, is called *foraging*. As the above example already sketched the plethora of possible search strategies that we and other animals might

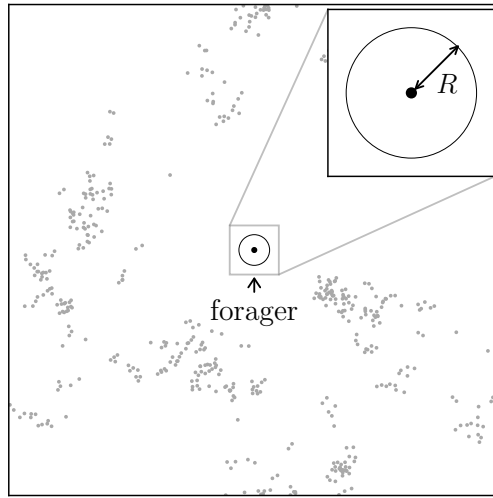


Figure 1.1: Illustrative example of a forager in a patchy resource landscape. The forager (black dot) can detect resources (gray dots) within a detection radius R . Note that resource locations are (often) not known *a priori*.

employ, the concept of *optimal foraging* has been extensively studied in the last few decades, starting with the seminal works of Charnov in 1976 [1] and Pyke et al. in 1977 and 1978 [2, 3].

Optimal foraging theory (OFT) assumes that animals optimize their (search) behavior in order to optimize for some type of *currency*, which is typically energy related¹ [4]. In general, the currency relates to biological *fitness*, of which higher values are preferred by individual foragers. Hence, natural selection results in ‘optimal foragers’ with foraging strategies that maximizes the fitness [3, 5, 6]. Obviously, animals are subject to a wide variety of factors that heavily influence optimal foraging behavior, such as cognitive capabilities of the animal (i.e., can the animal learn?) [7–11], what kind of information is available to the forager (e.g., resource sensing) [2, 12–14], and possible social aspects (i.e., can foragers interact with others?) [15–19]. Additionally, and perhaps most importantly, optimal foraging strategies strongly depend on the resource landscape [20–23], and animals must take resource density (availability) and temporal resource dynamics (predictability) into account if they are to survive. As foraging is ubiquitous among the living, one might mistakenly consider it a mundane task, yet the above examples highlight foraging as an incredibly complex decision process. Moreover, it is precisely its ubiquity that foraging is of interest to many scientific disciplines ranging from neuroscience [24], to

¹Note that energy expenditure is often related to time spent searching or the distance traveled during searches.

ecology [25], to mathematics [26], and many others.

Understanding complex decision process, such as those underlying foraging behavior, allows researchers to mimic natural systems as to apply (near) optimal strategies in artificial systems, giving rise to *bio-inspired* research [27]. A prime example of a successful bio-inspired approach are the now widespread artificial neural networks [28], that have displayed incredible applicability due to the recent increases in data availability and computational power [29]. Similarly, there has been a notable focus towards artificial foraging systems [30–33], as artificial systems (e.g., robots) become both more sophisticated and affordable. Most interest in this regard, is aimed towards designing swarm robotic systems [34], mostly inspired by social insects such as ants and bees, but also by other taxa such as flocking birds and fish schools. In swarms, individuals are considered to be simple: it is the sum of many that realizes potentially complex behavior [31]. This display of *swarm intelligence*, where simple units can act coherently despite lacking centralized control, largely overlaps with OFT, as many animals forage in groups [10]. Hence, studying foraging in both natural and artificial systems allows both the understanding of complex decision making processes in natural systems, as well as translating these to be applied in optimized artificial systems. As of now, the most cited applications of (swarm) foraging are optimizing searches for search-and-rescue missions [35, 36] and autonomous collection of resources on distant planets [37–39].

Instead of studying and designing (near) optimal artificial systems for specific foraging-related tasks, this dissertation instead takes a more fundamental approach and studies questions regarding different incentives and factors that influence optimal foraging behavior.

1.2 Resource distributions

As briefly touched on above, the resource landscape heavily impacts optimal foraging behavior. For example, when resources are plentiful, intricate behavior is often unnecessary as resources are encountered frequently [40]. In contrast, when resources are difficult to locate, intelligent foraging strategies become more important, as foragers can starve if they do not find resources in time. While spatially homogeneous environments that contain vast amounts of easy to locate resources exist (e.g., a cow grazing in a field), most natural systems instead have resources be sparsely distributed, sometimes tied to seasonal availability. Moreover, resources are often found to exhibit spatial heterogeneity, as they are distributed into patches, or display scale-free, fractal-like patterns of aggregation [41–53]. As such, statistical modeling approaches, including the ones presented in this dissertation, consider both patchy aggregates [54–57], as well as the more complex fractal patterns [23, 53, 56].

As different spatial features of the resource distribution will be tackled in this dissertation, a few comments on the different types of resource distribution models are in order.

1.2.1 Resource distributions: spatial characteristics

In field studies, it is difficult to generate complex resource patterns in experiments with real animals. As a result, these studies have often resorted to distributing resources within (fixed-size) patches (see e.g., [58]). In contrast, computational approaches, such as those presented in this dissertation, are not limited in this regard, and can therefore consider more complex resource distributions (see e.g., [23]).

In general, it has been commonly accepted that homogeneous, uniform distributions are unlikely to describe realistic spatial resource distributions. More specifically, initially homogeneous resource distributions display increased heterogeneity over time as an effect of landscape irregularities, self-organization, interactions, and both intra- and interspecific effects [59–64]. Despite the overwhelming evidence in favor of spatial heterogeneity, OFT has been studied extensively in cases where resource distributions were considered to be uniform (see e.g., [18, 40, 65–75]). However, studying such systems is not necessarily futile, as they can provide insights on optimality of different foraging strategies that are decoupled from more intricate effects of resource distributions. However, we argue here that, going forward, it becomes increasingly difficult to assume non-patchy, uniform distributions, as the evidence in favor of heterogeneous distributions accumulates (see Fig. 1.2 for illustrative examples).

1.2.2 Resource dynamics: temporal characteristics

Obviously, most natural resource distributions are not static, but exhibit temporal changes, where the source of these changes can differ drastically.

First, it is important to discuss how foraging itself can underlie temporal changes within resource distributions. Generally, foraging falls into two categories: non-destructive and destructive foraging [40, 76]. As the name implies, non-destructive foraging considers resources that can be revisited indefinitely. While perhaps unintuitive, Viswanathan et al. [40] argue that there exist natural systems wherein foragers exhibit this type of foraging, namely those wherein resources become only temporarily unavailable, i.e. those where resources (quickly) regenerate. Additionally, forager satiation can result in foragers leaving patches that are potentially still rich in resources. In contrast, destructive foraging considers foragers that consume the resource, e.g., prey consumption by foraging predators. Therefore, it implies time dependent spatial characteristics of the resource distribution of which the underlying cause is the consumption and regeneration of resources. To understand this, consider that when modeling foraging systems, it is often of interest to study specific incentives, such as the foraging

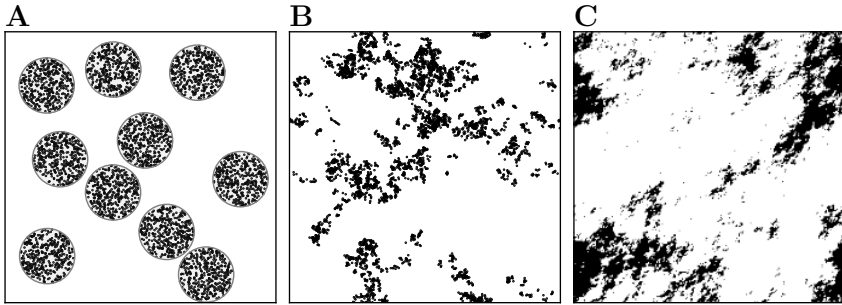


Figure 1.2: Illustration of the different resource distributions studied in this dissertation. (A) Resources are aggregated (clumped) in patches and resources do not exist outside of the patches. (B) Resource distribution that displays scale-free, fractal-like patterns, where clustered aggregates are surrounded by (potentially) vast areas void of resources. (C) Fragmented resource landscape.

efficiency, as function of resource heterogeneity. Essentially, such modeling approaches vary specific parameters that only change these assets of interest, while keeping all other characteristics constant. For example, if one is interested in the effect of resource fragmentation *per se* (see below), resource density should remain fixed – a widely employed tactic in works regarding fragmentation (e.g., [77–80]). Hence, when resource density is to remain fixed, destructive foraging implies immediate regeneration of a new resource upon consumption [23, 66]. Note that the new spatial location should not be the same as the old one, as that would make the foraging non-destructive instead. In general, whereas non-destructive foraging allows one to model resource distributions as static distributions, destructive foraging implies either a reduction in the number of resources (depletion) or indicates different spatial regeneration of resources that result in temporal changes in the resource distribution (dynamics). Note that both types of foraging have been studied extensively, and that it is known that they display vastly different optimal foraging strategies [40, 65, 66].

Finally, it is important to note that different causes can induce temporal changes in resource distributions. For example, there exist systems wherein resources are only temporarily available [81, 82], or where resources themselves are evasive, e.g. in predator-prey systems [65, 83]. Additionally, loss of habitat, and thus possible reduction in resource availability, has received considerable attention as it often results from anthropogenic influences and presents a major threat to the longevity of animal populations across the globe [84–86]. Habitat loss typically results in increased fragmentation [79], a process wherein habitable zones become increasingly smaller and more spatially separated [87, 88]. As a result, it greatly affects foraging behavior, as forager movement becomes necessary

to ensure population stability [89–91]. In general, it is important to distinguish between different causes of resource dynamics, as they drastically impact optimal foraging behavior and, subsequently, ecosystem stability.

1.3 Random searches

As described above, environmental characteristics shape optimal foraging strategies, most notably the foragers' movement strategy, also called *dispersal*. In general, it is assumed that resource locations are not known *a priori*, and hence foragers need to resort to random searches. Viswanathan et al. [92] define the random search problem as searching for an answer to the following question: “*What is the most efficient strategy for searching randomly located objects whose exact locations are not known a priori?*” A definite answer to this question is not easily obtained. In essence, the random search problem is at the base of nearly all foraging tasks and is required even when foragers are extremely clever. It corresponds to *exploration*, where new resource locations have to be discovered before other intricate mechanisms, such as learning, can take place.

1.3.1 Random walks

As the name implies, random searches are inherently random. As such, *random walks* are at the basis of random searches. The term ‘random walk’ was first used in a letter by the statistician Karl Pearson in 1905 [93], who asked a solution to the now well-known drunkard problem. In this problem, a drunk person starts from some starting point and walks a fixed distance ℓ in a straight line before turning through a random angle θ , after which the process is repeated n times. Pearson was interested in the probability of the drunkard ending up at a particular location from its starting point. For this particular problem, the answer was provided by Lord Rayleigh merely a week later², and sparked a vast interest on random walks across many fields of science.

Interestingly, many random walks are not necessarily described by an underlying stochastic process [95]. A well-known example of this is Brownian motion, where small particles deterministically collide with even smaller particles, resulting in seemingly random displacements. In the same vein, while the decision process that underlies forager movement might not be random, it can be described as a particle undergoing a random walk, and thus is amendable to techniques from the domain of statistical mechanics [76]. Interestingly, Brownian motion and other closely

²Rather amusingly, in my opinion, Lord Rayleigh was able to provide the answer so quickly because he solved this particular problem a few decades earlier in the context of moving sound waves. This illustrates that studying random searches require an interdisciplinary approach as they are applicable in many fields of science, which includes (optimal) foraging. While interdisciplinary studies are now increasingly common, at that time Pearson eloquently wrote [94]: “... one does not expect to find the first stage in a biometric problem provided in a memoir on sound.”

related random walks such as the Ornstein-Uhlenbeck process [96], have been additionally applied in economics [97], as stock prices appear to follow similar trends as particles and foragers.

In general, when random walks of many particles (foragers) are considered, they represent a *diffusion* process. Diffusion is the process by which particles *diffuse* from regions with high concentrations to low concentrations. An example of this from daily life is when one considers a blue ink droplet that is dropped in a glass of water. Over time, the highly concentrated ink particles will diffuse, and as a result the water will turn blue. As one can, in principle, track positions of individual particles over time, diffusion is nothing more than the process of many random walks by (non-)interacting particles. Throughout this dissertation, foragers will be discussed within this context as well (see also [76, 98]), where highly diffusive foragers (those that quickly move away from the starting point) represent foragers with a different random search strategy compared to slowly diffusing foragers. As diffusion has been extensively studied in physics, it should come as no surprise that many theoretical advances in OFT originate from studies on nonequilibrium statistical mechanics [76, 92, 99–101].

As random walks consider probabilistic displacements of particles, quantities that are often of interest outside of the probability density function (pdf) are its moments and the *mean squared displacement* (MSD). More formally, let $x(t)$ describe the position of a particle at time t that started at x_0 at $t = 0$. Then $p(x)$ defines the probability of finding the particle at some location $x + dx$, with its corresponding n th moment

$$\langle x^n \rangle = \int_{\mathcal{D}} x^n p(x) dx \quad (1.1)$$

over the domain \mathcal{D} (which is typically $[-\infty, \infty]^d$, where d the dimensionality of the system). The MSD is defined as

$$\text{MSD}(t) = \langle |x(t) - x_0|^2 \rangle, \quad (1.2)$$

where $\langle \cdot \rangle$ denotes the *ensemble* average over many particles. In other words, the MSD denotes the expected (or average) squared displacement from a reference location x_0 . In foraging, the MSD is useful as it captures how much of an environment has been explored, i.e. how much of the environment has been covered at a time t [102].

Let us briefly consider an simple example: one-dimensional Brownian motion. The pdf of a particle undergoing Brownian motion starting at the origin $x_0 = 0$ is a normal distribution with mean (first central moment) of 0 and variance (second central moment) $2Dt$, where D is the *diffusivity*, i.e. the rate of diffusion that, in case of particles, depends on the medium. For Brownian motion, the MSD is equal to the variance. As such, Brownian foragers are most likely to be found close to where they started, which

already indicates that this might in some cases be a suboptimal random search.

In the context of area coverage (exploration) of an environment, random walk theory predicts that the MSD of diffusing particles scales as

$$\text{MSD}(t) \sim t^\mu, \quad (1.3)$$

where μ depends on the type of diffusion. So-called ‘normal’, or *Fickian*, diffusion describes processes where the MSD scales linearly with time, i.e. $\mu = 1$. Brownian motion is the simplest example of normal diffusion. In contrast, *anomalous* diffusion arises when $\mu \neq 1$, splitting into *subdiffusive* ($\mu < 1$) and *superdiffusive* ($\mu > 1$) processes [66]. The fastest possible diffusion is realized when particles execute straight-line motion, called *ballistic motion*, where $\mu = 2$. From the area coverage description of the MSD, it is not hard to imagine that superdiffusive foragers might search more efficiently.

Although in the early stages of theoretical ecology it was implicitly assumed that the standard assumptions underlying equilibrium statistical mechanics would hold for foragers as well, it has been argued that it provided “*convenience rather than applicability*” [103]. Effectively, it meant that early studies into foraging behavior regarded movement to be described by normal diffusion, while many foragers often display different types of diffusion. More specifically, the diffusion characteristics of foragers are often resulting from complex interactions, such as attraction towards other foragers [104–108], home ranges observed in central-place foragers [109–113], memory [8, 9, 11, 57, 114], and many others. As such, nonequilibrium statistical mechanics better describes foraging systems [76], which critically applies to the random search behavior as well.

1.3.1.1 Lévy walks

As in all fields of science, OFT has profited from advancements in other fields. Most notably, improvements in data logging techniques have resulted in ascribing anomalous diffusion to foraging organisms [40, 51, 115]. More specifically, the pdf of their subsequent flight lengths – the lengths during which their angle of direction remains constant (see, e.g. [66]) – has a diverging second moment compatible with the generalized central limit theorem devised by Paul Lévy in 1939 [116]. It is therefore that these superdiffusive movements of foraging organisms are called *Lévy flights* or *Lévy walks*.

Before we move on, it is important to distinguish between *flights* and *walks*, as they define vastly different movement models. Lévy flights are random walks wherein displacements occur with infinite velocity, i.e. there are instantaneous ‘jumps’. On the other hand, Lévy walks consist of foragers walking along the sampled flight lengths with a (finite) fixed velocity v_0 , thus giving rise to a spatio-temporal correlation in forager move-

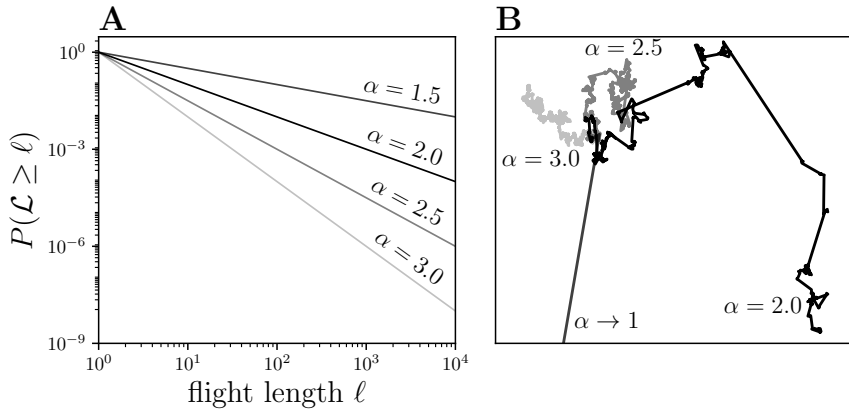


Figure 1.3: Illustration of characteristics of Lévy walks for different Lévy parameters α . (A) The complementary cumulative density function $P(\mathcal{L} \geq \ell)$, which defines the probability of sampling random flight lengths \mathcal{L} larger or equal than ℓ . (B) Typical Lévy walks as generated by sampling flight lengths from a power law distribution and uniform angles.

ment [98]. Although flights with infinite velocity are unnatural by definition, they are generally more analytically tractable and have therefore been studied extensively. Nonetheless, the study of Lévy walks pertains to more realistic ecological frameworks, as indicated by the number of OFT studies that consider Lévy walks over Lévy flights.

Lévy walks are characterized by heavy-tailed power law distributions over flight lengths ℓ (Fig. 1.3), with a Lévy parameter α ,

$$p(\ell) \sim \ell^{-\alpha}. \quad (1.4)$$

In general, it is assumed that the direction of travel for each flight is sampled uniformly (but see e.g., [66]). For $\alpha \leq 1$, it can be easily verified that the pdf cannot be normalized. Then, in the limit of $L \rightarrow \infty$ and for $\alpha > 1$, Lévy walks encompass distinct modes, depending on the specific value of α . First, as $\alpha \geq 3$, the second moment does converge, and the above distribution describes normal diffusion (Brownian motion). For $\alpha \rightarrow 1$, we recover ballistic (straight line) motion as flight lengths approach infinity. For intermediate values $1 < \alpha < 3$, foragers exhibit anomalous diffusion with superlinear scaling of the MSD. This type of diffusion effectively describes foragers that interchange localized movement with rare, but statistically relevant, long-range displacements (see Fig. 1.3 for examples and [98] for an extended discussion on Lévy walks).

In the seminal work of Viswanathan et al. in 1999 [40], they illustrated that Lévy walks with $\alpha \approx 2$ are the optimal random search strategy for a single forager in environments where resources were scarce and

spatially uniform. In the years following this result, the robustness of Lévy walks as an optimal random search has been widely established [23, 54, 55, 65, 66, 83, 117]. However, despite these models supporting the occurrence of Lévy walks in a foraging context, whether organisms truly execute Lévy walks is currently still debated [118–123]. Nevertheless, evidence from natural systems that exhibit Lévy walk behavior is accumulating, and Lévy walks have been observed in a wide variety of systems ranging from cancer cells [124], T cells [125], micro-organisms such as bacteria [126], insects such as honey-bees [127], birds such as the albatross [115], many aquatic animals [51, 128], mammals such as deer [129, 130], and even human hunter-gatherers [131].

1.3.1.2 Lévy flights as resource distributions

Before moving on towards more intricate search strategies, we would like to mention that the above Lévy flight description can additionally be used to describe spatial resource distributions, as in [23]. Therefore, resource-to-resource distances have often been observed to follow an inverse power law as well, either as a result of passive dispersal [51, 132, 133] or, for example, seeds being dispersed by frugivores (see [134] for a recent review). This gives rise to so-called *Lévy dust* distributions [53, 135], which provide a simple way of simulating scale-free, fractal-like distributions (see Fig. 1.2).

1.3.1.3 Intermittent and adaptive searches

Whereas Lévy walks have been widely accepted as a sound random search strategy, many organisms actually adapt their searching behavior depending on their internal state [1, 136, 137] and external (often environmental) influences [128, 138, 139]. This is often a result foragers being effectively ‘blind’ [40, 71, 72], as the resources they are looking for are often detected only up to a few body lengths. As such, long displacements such as those encountered in the Lévy walks described above, often carry with them a low resource detection probability. To this end, many animals exhibit *intermittent searches*, where localized, slow and thorough exploration that allows resource detection, is interchanged with fast relocations during which resources cannot be (easily) detected [140, 141] (and see [142] for an extensive overview).

Interestingly, Lévy walks themselves seem to contain similar behavior depending on α . Most notably, as visible in Fig. 1.3, for $\alpha = 2.0$, the foragers’ trajectory displays intermittent-like search behavior. However, it must be noted that while the trajectory appears as if the search is intermittent, the behavior of the forager does not structurally change, and detection is equally likely regardless of where along the trajectory the forager is. Therefore, ‘true’ intermittent searches imply a structural change in behavior, e.g. a change of α , when a certain condition is met.

In general, conditions that trigger a behavioral change are plentiful. In this dissertation however, as we are most interested in the impact the re-

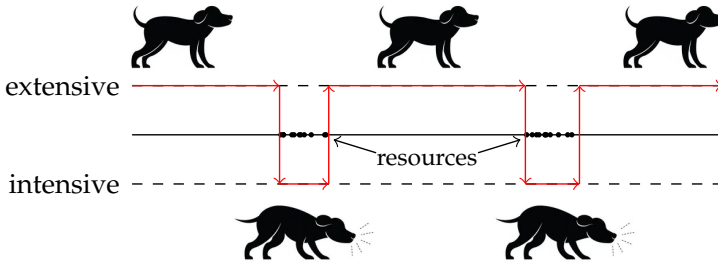


Figure 1.4: Illustrative example of a forager displaying adaptive search behavior in a one-dimensional patchy resource landscape. Switches from extensive to intensive searches are triggered by resource detection. In turn, switching back to extensive searches occurs when patches are exhausted.

source distribution has on optimal foraging behavior, we attribute the intermittence to *patch detection* (see Fig. 1.4). Note here that our definition of intermittence, differs from the usual definition, e.g., as used by Bénichou et al. [142]. The difference is that common terminology refers to intermittence with fixed rates of switching search behavior, i.e. independent of the current state of the forager, whereas we let this switch be state-dependent. The reason for this difference is that natural environments often have patchy resource distributions and, as such, finding a resource typically indicates the presence of others nearby. Therefore, it is not hard to imagine that more thorough local searches should be triggered by resource detection [143]. This can, for example, be modeled as a Lévy walk that changes its α to display less diffusive behavior, as to keep the forager close to (or within) the patch rich in resources, making future resource detections more likely to occur. Hence, the effectiveness of intermittent searches relies heavily on the resource distribution.

1.3.2 Informed walks

As organisms grow more complex, they can forego random searches in favour of more informed search strategies [144–146]. This type of adaptation relies on several factors, such as the learning capabilities of the forager and the predictability of the environment [147, 148]. Obviously, advantages of learning (such as memory) disappear when the environment becomes highly unpredictable. Hence, as one would intuitively expect, memory has been found to be more advantageous in environments that are more predictable [149].

Even though environments might be predictable, most studies implicitly assume no prior knowledge to be available to the forager. This makes initial exploration of critical importance to the speed at which a predictable environment is learned. This gives rise to an important problem in many fields of study, particularly those related to learning: the *exploration-*

exploitation trade-off [150]. In a foraging context, the trade-off is encountered, for example, in ant colonies deciding on a new nesting site [151, 152], or when foragers have to decide whether to exploit current known patches in favour of searching for patches of potentially higher quality. While the trade-off can most often not be explicitly solved, it should be noted that within the context of foraging, survival is most often more important. As such, simple models wherein foragers are more likely to exploit their current knowledge when not having encountered resources in some time have been shown to be effective [23, 73].

What and how foragers can learn depends strongly on the cognitive capabilities of the forager. Whereas relocations to known patch locations have been observed [153, 154], simpler schemes such as a (short-term) memory of the number of encountered resources [23] or maintaining a general direction (biased towards known patches) [155–157] can also be considered. Importantly, this non-exhaustive list of examples illustrates a more general result: regardless of the memory model, memory has the potential to be beneficial in a predictable environment.

It should be noted that maintaining any memory model introduces additional costs, i.e. increased metabolic rates [158], that foragers need to account for. As a result, benefits of memory depend strongly the complexity of the environment. For example, in very simple environments, benefits of maintaining a complex (spatial) memory simply do not outweigh the expected costs [148].

1.4 Foraging in groups

The previous section considered possible strategies that single foragers can use as to optimize their foraging efficiency. Besides this individual optimization, foragers that are contained within a group might be able to benefit from interactions with conspecifics. As an example, one can imagine that in a cohesive group, the search for difficult to find resources can effectively be parallelized. Obviously, group foraging is a complex process, as group sizes span several orders of magnitude: from two loosely connected individuals to extremely large aggregates [159–161]. Foraging in groups additionally regards a task for which optimal strategies are straightforwardly transferred to practical applications, ranging from designing a group of artificial agents (e.g., robots) that search for resources [38] (as in the aforementioned search and rescue missions [35, 36]), to implementing optimal decision making in swarms [162–164].

Foragers can interact with each other in many different ways (see Fig. 1.1). In general, interactions facilitate an exchange of information. For example, (long-range) vocal signalling between individuals is widespread in the animal kingdom (see, e.g., [165–169]). Other methods, such as the pheromone trails left by ants [170], enable information sharing through indirect communication – a mechanism called *stigmergy* – and has been

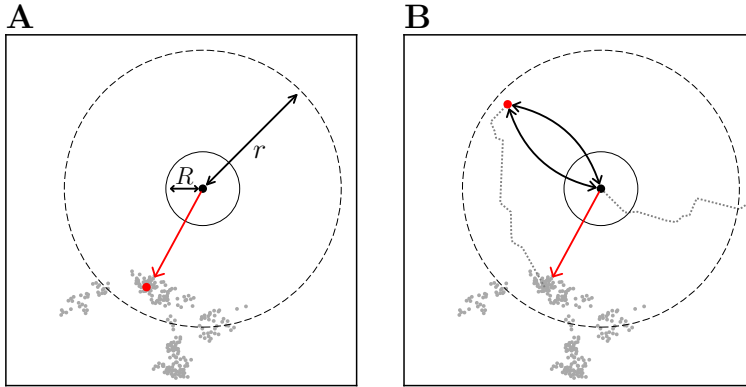


Figure 1.5: Illustrative examples of foraging in groups. Straight black arrows indicate resource detection radius R and conspecific interaction radius r . Note that, typically, $r > R$. Dotted trajectories indicate past movement, e.g. a Lévy walk, of the focal forager (●) and a conspecific (●). Straight red arrows indicate future movement of the focal forager towards the patch with resources (●). (A) Group foraging scenario wherein a forager joins successful conspecifics on a patch. Note that this behavior is strictly *competitive*, as resources on the patch need to be shared with conspecifics (see text). (B) Collective foraging scenario where information (here; the location of a patch) is shared between conspecifics, as indicated by the curved arrows, in order to facilitate the collective. Note that this behavior is strictly *collective*, as it implies altruistic behavior of information sharing (see text), and that this can occur off-patch.

widespread attention in artificial systems (see, e.g., [33, 171–174]). How individuals, or the group as a whole, can benefit from interactions, and how these benefits depend on individual decisions as well as environmental constraints, is not yet fully understood.

Before proceeding, we would like to note that foraging in groups does not necessarily imply cooperation, but can additionally imply competition. However, the terms *group foraging* and *collective foraging* have mostly been used interchangeably, e.g., as seen in [106, 107]. In this dissertation, we argue that one should make a clear distinction between the two, as they refer to two vastly different phenomena.

In general, we argue that *group foraging* should pertain to the study of groups of inherently selfish foragers. Thus, individual foragers do not necessarily optimize their behavior to favour the group as a whole, but instead optimize individual gain, hence assuming the *selfish herd hypothesis* [175]. Note that while individual optimizations might lead to optimization on the group-level, this is not always the case [21, 176–179]. Examples of group foraging are systems wherein intraspecific competition is either explicit, e.g. fighting for patch dominance [180, 181], or implicit, e.g. through

competition for a limited set of resources [21, 176, 178].

In contrast, we define *collective foraging* as a group of altruistic foragers, where individuals act as to serve the collective. Such an altruistic framework is often assumed to underlie (artificial) swarm systems [31, 182]. Again, optimizations on the level of the collective may result in individual optimizations, however this is not a requirement. Examples of collective behavior in collective foraging are active inhibition of visitation to exhausted patches [183], task allocation-like structures [184, 185] and (active) recruitment towards patches [186–188].

1.4.1 Group foraging

Group foraging has been studied in the context of so-called *information-sharing* systems [16, 18], where interactions are often assumed to be limited to continuous monitoring of (nearby) conspecifics. As resource environments are often patchy (see Section 1.2), individuals can benefit from joining others that are observed to have been successful [67, 189]. Of course, it can occur that more intricate behavior is displayed. Examples of such behavior are on-patch competition, e.g. fighting over limited resources [21, 190–192], kleptoparasitism [193–195], or, in contrast, social resource sharing among individuals [196, 197]. Formation of aggregates on patches rich in resources can also provide increased individual foraging successes through synchronizing foraging bouts [198–200], which interestingly have been observed even in mixed-species systems [201–204].

Different models discuss groups of foragers as *producer-scrounger* systems [15, 205–207], in which individuals are considered to be either a producer or a scrounger. In its essence, producers are those that are taken advantage of by the scroungers [208]. Obviously, the effectiveness of both strategies depends on the number of producers relative to the number of scroungers. While information-sharing and producer-scrounger frameworks are extensively studied, both idealistic models are unlikely to capture realistic settings in full detail. As such, more research is needed in either combining the two models, or potentially devising novel models, as to describe observed natural phenomena in foraging groups.

We would like to emphasize that, while it might appear that potential foraging advantages act as the evolutionary pressure leading to group-level behavior, one should be careful by attributing this solely to foraging. In particular, living in groups – not necessarily foraging – already provides individual benefits such as decreased predation risk [161, 175, 209], possibly due to changes in individual vigilance [210–212]. However note that, for example, decreases in individual vigilance often increases the time spent foraging [21, 213] (but see [214]), thereby additionally contributing to foraging advantages.

1.4.1.1 Origins of competition and group foraging.

As explained above, group foraging pertains to the study of foraging in groups that are inherently competitive. Most often, this is the result from the limited number of resources available on patches, as these need to be shared among all foragers. In our particular interest are systems where this competition is implicit, i.e. there is no active competition, yet individuals are competing for the same set of resources for which ‘first-come-first-serve’ applies. These systems are thus comprised of destructive foraging events, and hence are applicable to the study of dynamic resource landscapes. Individual foragers have to make decisions whether to join others or not, often based on several factors, such as the estimated time to detect patches and on-patch resource availability [67, 215]. Obviously, when resources are plentiful, individuals do not need to join others as their own random searches amount to high resource intake rates [105]. Additionally, benefits of joining others depend critically on the estimated or observed (local) forager densities, as these correspond to higher levels of on-patch competition as group sizes increase [21, 108, 176–179, 216]. As such, group formation, while providing some individual benefits under specific circumstances, is not generally advantageous towards foraging optimally.

1.4.2 Collective foraging

On the other hand, collective foraging pertains to the study of foraging in groups that are inherently collective, i.e. they should display some degree of altruism. Altruistic behavior is introduced to group foragers by having them explicitly communicate information, e.g. on specific patch locations. Note here the subtle difference between informing conspecifics on a patch location (which can occur off-patch) and attraction towards a (nearby) conspecific (that can only occur on-patch). Thus, how information dissemination occurs within collective systems greatly affects the benefits of altruism. Obviously, when others are difficult to communicate with (e.g. when forager densities are low or communication ranges are short), foragers can waste valuable time looking for others, thereby decreasing the benefits of altruistic behavior. To this end, as many (both real and artificial) collective systems exhibit short communication radii [31, 182], they often resort to nesting sites wherein forager densities are high [217–219]. Especially the latter is typical for ant and bee colonies, where they display highly intricate communication patterns for information transfer, such as the waggle dance performed by bees [184, 185, 220].

When nesting sites are not available however, active information transfer is aided by formation of ephemeral aggregations [167, 221], including those on the patches rich in resources [1, 222]. These type of aggregations are often studied under the name of *fission-fusion dynamics*, where social interactions with different conspecifics take place on the patches [223–225]. In principle, these interactions result in a (dynamic) interaction network,

i.e. a graph, of which the structure highly influences the collective response to environmental stimuli. The interaction networks or graphs, observed in natural systems can take various forms, such as scale-free networks [32, 75, 226], and can rely on topological distances to nearby conspecifics [227, 228]. While one might intuitively guess that fully connected networks, i.e. allowing individuals to communicate with everyone, benefit the information transfer in collective systems, this is most often not the case. As an example, when collective responses need to be rapid, communication with a lower number of individuals has been shown to optimize response times [229–231]. This is of particular interest to collective foraging scenarios, as decisions should not take too long when environments are (highly) dynamic for foraging to be efficient.

1.4.2.1 Origins of cooperation and collective foraging

The evolution of cooperation, ultimately leading to collective systems, has been regarded as a major transition in evolution [232]. It is clear that under specific circumstances, individuals can benefit from cooperation through *inclusive fitness* [233]. Within the context of (collective) foraging, cooperation might increase foraging efficiency, e.g. when large groups of cohesive foragers experience increased foraging successes [234, 235]. Additionally, foraging predators might require a minimum group size in order to take down large prey [197, 236]. In general, reasons for cooperation are plentiful, but one should be careful by attributing foraging benefits as the main driving force behind collective behavior.

1.5 Foraging and population dynamics

While up until now we have not explicitly discussed demographic events, such as death and reproduction of both foragers and resources, in real natural systems these features cannot be ignored when time scales exceed the expected lifespan of the organisms. Therefore, we argue here that when one studies foraging on appropriately large time scales, explicit population dynamics must be included. Both to the understanding of natural systems and the applications within artificial systems, unraveling population-wide dynamics, such as species survival, is of great ecological importance [237]. Most interestingly, very recent studies have started to integrate movement patterns from OFT into population models, e.g. Dannemann et al. in 2018 [238], as it is known that species dispersal significantly affects ecosystem stability [91, 239]. Moreover, as nearly all animals forage for survival, changes in landscape ecology shape the very future of life and biodiversity across the globe.

In particular, rapid anthropogenic changes to global systems are of increasing concern. As an example, the Amazon forest has seen extensive deforestation, where almost 20% of the forest has been cut down as of

writing this dissertation [240, 241]. As these rainforests house an incredible amount of species [242, 243], loss of habitat as a disturbance has long-lasting (potentially irreversible) effects on the global climate and loss of biodiversity [240, 244–247]. Moreover, many ecosystems across the globe display increased levels of fragmentation [77, 79, 85, 86, 248], most often caused by human action such as the aforementioned deforestation [249]. Here, fragmentation refers to the process wherein habitable zones become both smaller and more spatially separated [77] (see Fig. 1.2).

As these changes are typically observed on scales much faster than species can adapt, both habitat loss and subsequently fragmentation are of specific interest to ecologists. Therefore, we argue that modeling efforts that aim to identify the effects of landscape degradation on population dynamics of its inhabitants are of increasing importance.

1.5.1 Lotka-Volterra systems

For modeling population dynamics, an extensively studied system is the *Lotka-Volterra* model, introduced independently by both Lotka [250] and Volterra [251] in the 1920s, as a deterministic set of two coupled non-linear differential equations. The equations describe the temporal evolution of a system comprised of predators and their prey. Note that, within the context of foraging as discussed in this dissertation, predator and prey populations are represented by foragers and resources, however, these are most often referred to as *predator-prey* models.

Historically, as fur trappers of the Hudson’s Bay Company had extensive records of the number of pelts harvested each year, they observed regular oscillations in the number of pelts originating from hare and lynx between the years of 1821 and 1914 [252, 253]. These oscillations are a direct effect of predator-prey interactions. As the number of prey increases, the system supports more predators, which in turn increase predation pressure leading to decreases in prey population and subsequently predator population; a process that repeats with cycles often of fixed lengths [254, 255]. It were precisely these oscillations that could be modeled by the Lotka-Volterra system, which is why it received considerable attention in fields such as biology, chemistry, physics and mathematics [256–262]. Note that, despite it being one of the foundational works on modeling population dynamics, the original Lotka-Volterra system presents some unrealistic features and has been shown to be mathematically unstable [259, 262–265].

In brief, we shall discuss a simple two-species Lotka-Volterra model: the classic predator-prey model. Recall that the bridge to foraging – on which this dissertation focuses – is straightforward when regarding the foragers as the predators and the resources as the prey. The model describes the time evolution of predator density $x(t)$ and prey density $y(t)$

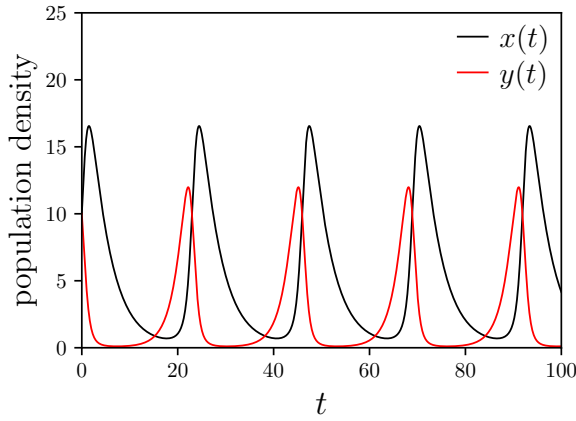


Figure 1.6: Example of oscillations obtained using the two-species Lotka-Volterra model for $\lambda = 0.1$, $\mu = 0.25$ and $\sigma = 0.5$, and initial population densities $x(0) = y(0) = 10$. Note that this example highlights one of the models' unrealistic properties, in that populations can consist of less than 1 organism, yet are able to recover (see e.g., [265]).

as

$$\frac{dx(t)}{dt} = \lambda x(t)y(t) - \mu x(t), \quad (1.5)$$

$$\frac{dy(t)}{dt} = \sigma y(t) - \lambda x(t)y(t), \quad (1.6)$$

where λ , μ and σ the predator-prey interaction rate, predator mortality rate and prey reproduction rate respectively. Depending on the values of the demographic rates, oscillations in population numbers can be observed (see Fig. 1.6). A more thorough description of the Lotka-Volterra system would take considerable more effort, and is therefore considered to be well beyond the scope of this dissertation.

1.5.1.1 Forager movement and Lotka-Volterra systems on lattices

Whereas the simple system above provides an elegant model of population dynamics, it does not contain explicit spatial dependence. However, as discussed in Section 1.2, resource landscapes (habitat) often exhibit some form of spatial heterogeneity. As to capture landscape characteristics, the above system has been translated to represent population dynamics on specific sites within a lattice. Lattice-based models, such as the Ising model [266], have been the subject of many studies in the field of statistical physics, making them able to capture the spatial structure prominent in natural systems while remaining amenable to both analytical and computational

methods [238, 263, 267–269]. Within the context of foraging, it models systems of foragers and resources existing on sites of a lattice, and allows foragers to ‘hop’ to other (neighboring) sites. Additionally, death and reproduction are modeled as creation and annihilation processes [263].

Most interestingly, inclusion of spatial structure immediately results in (local) ‘pursuit and evasion’ patterns in predator and prey densities. This can be explained similar to the cycles observed in natural systems, where areas rich in resources are invaded by predators (pursuit) and prey reacts by inhabiting empty surrounding sites (evasion) [263, 270, 271]. Moreover, intricate spatial patterns can arise while applying simple rules, such as spiral and fractal patterns [272–277]. Obviously, the rate of diffusion of both predator and prey highly influences the stability of the ecosystem [278]. As an example, slowly diffusing prey populations can be more easily subjected to local extinction if predators are highly diffusive, especially when prey are reproducing slowly [100, 279]. When we can assume both predators and prey to be reactive, i.e. through adaptation of their diffusion rate, how species respond to local extinction events has only recently begun to be unraveled (see, e.g., [238]).

1.6 Applications of optimal foraging

We believe a discussion on application potential of the rather fundamental work presented in this dissertation is warranted.

For computer scientists, applying results from fundamental studies on biological systems has historically provided us with numerous technological advances (e.g., [280]), and the field of *biomimetics* grows ever more popular (see [281] for a review). Our results can potentially be taken into account when designing (decentralized) controllers for autonomous (foraging) systems such as swarm robotics [31, 32, 182, 282–285]. Within swarm robotics, we find a plethora of applications ranging from efficient collective transport to systems that can self-organize [286–288]. Additionally, optimizing collective foraging can aid in the mapping of hazardous environments by efficient exploration [289, 290], provide efficient searches of patches of interest (e.g., pollution sources such as oil spills [291] and weeds [292, 293]), and can substantially improve success of search-and-rescue missions [36, 294, 295]. Another application – perhaps more futuristic – is the deployment of robot swarms on distant planets for planetary exploration [296].

Within the context of ecology and conservation planning, we argue that, as highlighted in Section 1.5, understanding foraging patterns in natural systems is invaluable to the conservation of those systems. Most importantly, modeling the effects of destruction and fragmentation of habitat might aid in the reversal of trends of declining biodiversity observed around the globe [237]. While some studies pertaining foraging and habitat loss exist [55, 238], the combination of applying OFT on the scale of pop-

ulations is relatively unexplored. To this end, the work in this dissertation provides a stepping stone for future studies into the complex interactions between landscape patterns, population dynamics and optimal foraging, and how these relate to global patterns and can help in the conservation of biodiversity.

1.7 Research questions

Foraging encompasses complex random search behavior with intricate, context- and state-dependent decision making. Although foraging research has developed and matured over the past decades, there exist many open questions regarding optimal foraging, of which some have been sketched above. In particular, this dissertation addresses an overarching question within foraging research: *How can foragers maximize their foraging efficiency, and how do optimal foraging strategies depend on different factors?* More specifically, we study how environmental conditions can shape optimal foraging behavior, with particular interest in the resource distributions presented in Section 1.2, and how they depend on (i) individual cognitive capabilities (memory), (ii) interactions with conspecifics and (iii) population-wide diffusion characteristics and (optimal) responses.

In order to address our main research question, we divide our work into four research questions that include accompanying hypotheses. Below, these research questions are iterated, including motivations for their selection.

Research question 1 (Chapter 2). *How can an individual forager benefit from spatial memory when resources are distributed within patches?*

As illustrated above, (spatial) memory is only beneficial in environments wherein resource distributions are predictable, at least to some extent. Instead of storing and recalling each individual resource location, as this quickly becomes unrealistic when the number of (encountered) resources grows over time, we propose to learn parameters of a spatial distribution that approximates the patchy resource distribution. Hence, if individual foragers possess the ability to learn a spatial distribution [10, 146, 297], they can exploit this by sampling goal states from memory [144, 145]. These goal states, given that the spatial distribution approximates the true distribution well, are then within the patches rich in resources with high probability.

Here, we argue that any memory component that is of any use to a forager needs to possess the following requirements (at minimum); (i) a spatial memory needs to be able to approximate the spatial resource distribution; (ii) it needs to allow for sampling, i.e. to inform where the forager will travel next; (iii) it needs the ability to be updated as to reflect possible changes in the resource distribution. Note that this additionally allows

the forager to forget, which is a necessary component as most organisms possess only limited (finite size) memory; and finally (iv) spatial memory needs to exhibit a way to express uncertainty, as it allows foragers to make decision based on the estimated correctness of their learned model.

To this end, we introduce an agent-based model wherein a forager is able to learn a spatial distribution by learning a Gaussian mixture model (GMM). As GMMs are universal function approximators [298, 299], and given that resource distributions are clumped (as in Fig. 1.2), they can be used to learn, in principle, any spatial distribution (requirement (i)). Additionally, sampling from GMMs is straightforward (requirement (ii)). Moreover, GMMs can be learned incrementally [300, 301] (requirement (iii)). Despite GMMs providing an excellent baseline for a spatial model in environments with clumped resource distributions, *when* the forager should exploit its knowledge is still a difficult decision. To this end, we instead let the forager learn an ensemble of GMMs, and let the likelihood of exploiting this ensemble model to depend the model uncertainty. As ensemble models consist of separate models learned on subsets of the data, the individual models can be used to estimate how ‘correct’ the resource distribution is approximated [302–304] (requirement (iv)).

Using the ensemble of GMMs as spatial memory, we consider foragers that display a hybrid foraging strategy wherein random searches are interchanged with informed searches towards goal locations sampled from memory. More specifically, random searches are truncated in favor of informed searches when the forager has not encountered resources in some time. We let this time depend on the uncertainty of the learned spatial distribution, and consider a scheme wherein random searches are more likely to be truncated the more certain the forager is.

To study the influence of the resource distribution and spatial memory on foraging efficiency, we subject a non-destructive forager to search for (detect) a large number of resources and measure the number of steps needed to complete this task. Then, we test the following hypothesis:

Hypothesis 1.1. *Spatial memory increases foraging efficiency by enabling revisitation of known resource locations (patches).*

Once a (small) subset of patches within the environment has been visited, the ensemble model converges to approximate this subset, and the forager continuously exploits this by visiting these patches. Hence, higher foraging efficiencies can be achieved, as more resources are detected in less time, simply by exploiting a known subset of non-destructive resources. Hence, strong use of spatial memory results in less diffusive behavior, effectively representing localized searches [57, 222]. Despite the obvious increase in foraging efficiency, when multi-objective searches are of interest, such a strategy is not necessarily advantageous as the forager is restricted to consuming resources of only a small number of patches. This can penultimately hurt the forager in the long-term, as many organisms

rely on the intake of different resources (e.g., food and water) in order to survive [54, 305–307]. More specifically, we study the patch diversity as the number of resources per patch as an indication of how well different patches are explored. Then, we arrive at the following hypothesis:

Hypothesis 1.2. *Spatial memory negatively affects patch diversity, and thereby potentially resource diversity as well.*

□

As stated earlier, learning a spatial model is only beneficial to a forager when the resource distribution is predictable. In Chapter 2, this is realized by having the forager perform non-destructive foraging, effectively rendering the resource distribution static. When foraging is destructive instead, resource distributions change rapidly necessitating the need for different search strategies, such as the adaptive searches discussed above. Hence, we now study systems where the resource distribution displays scale-free, fractal-like patterns (see Fig. 1.2). Additionally, as foragers are often not solitary, we shift the focus from the individual forager to a group of foragers that compete for resources within the environment. In this setting, this dissertation aims to seek an answer to the following question:

Research question 2 (Chapter 3). *How does resource fractality determine the effectiveness of group foraging strategies on groups subjected to intraspecific competition?*

While foragers can benefit from interactions with conspecifics to increase the (group) foraging efficiency [104, 107, 209, 221, 308], increased group sizes give rise to increased levels of intraspecific competition [21, 108, 176, 178, 179, 216]. Obviously, when patches are extremely rich in resources, large aggregations on patches can be supported. In contrast, patches that contain little resources increase levels of competition, making group-level strategies, such as joining successful others, less enticing. While both individual foragers in highly complex environments, and complex groups of foragers in simple environments have been studied extensively, a full quantitative description of the effects of group-level behavior (e.g., joining ranges) and resource distribution (e.g., degree of clustering) is missing.

To this end, we employ an agent-based model of a group of intermittent Lévy foragers that change their Lévy parameter upon resource encounter (as discussed in Section 1.3.1.3). More specifically, they interchange highly diffusive, *extensive* searches, with localized, *intensive* searches. Foragers are attracted to those that search intensively, as this type of search indicates the presence of a patch. In our model, we consider patchy resource distributions and resource locations are sampled as a Lévy dust (see Section 1.3.1.2). We use this relatively simple model to test the following hypothesis:

Hypothesis 2.1. *Attraction towards successful conspecifics is advantageous for individual foragers, but only when resources are sufficiently clustered and competition is not too fierce.*

When dealing with clustered resource distributions, resource intake rates among individuals are not necessarily uniformly (or normally) distributed. As one would expect, the forager that first detects a patch – or rather an area dense in resources (see Fig. 1.2) – will be able to consume more resources than others arriving at a later time. As Hypothesis 2.1 suggests, fierce competition, expressed by large group sizes, only increases resource inequality. As is often implicitly and intuitively assumed, a group benefits when each individual benefits (but see Section 1.4). However, individuals can benefit from group-level interactions while not necessarily increasing the group search efficiency, e.g., by reducing resource intake inequality. The reduced inequality effectively corresponds to a reduced variation of resource intake, and therefore the following hypothesis is considered:

Hypothesis 2.2. *Joining successful conspecifics in areas rich in resources decreases group benefits, but increases individual advantages as expressed by a reduced variation in resource intake.*

□

Despite most natural systems being competitive by nature, collective systems display the effectiveness of collective behavior. Most notably, while individuals of collective systems are often (relatively) simple, it is the sum of their parts that enables impressive feats [31]. In the context of foraging, we argued that collective foraging pertains to the study of altruistic behavior during a foraging task (see Section 1.4.2). Then, as to elucidate potential influences of the resource distribution, we ask ourselves the following question:

Research question 3 (Chapter 4). *How can altruistic behavior increase collective foraging efficiencies, and how does it depend on the patch persistence?*

To answer this question, we study collective foraging in patchy and ephemeral resource landscapes, and let individuals actively communicate with one another over (relatively) short distances. Initially, all foragers execute random Lévy searches, but they can switch to active recruitment of conspecifics after detecting a patch, instead of individually exploiting it themselves. However, not all patches should result in recruitment. When patch durations are short, it becomes increasingly difficult to encounter enough conspecifics, and it would have been better – both at the individual *and* collective level – for the forager to have exploited the patch by itself. Therefore, for such a recruitment scheme to be beneficial, we pose the following hypothesis:

Hypothesis 3.1. *The net gain of the collective should be estimated by a single forager, providing a threshold for displaying altruistic recruitment behavior.*

Note that estimating the net gain, i.e. how much the collective benefits from resource sharing, should explicitly contain the expected number of conspecifics to be encountered. Therefore, as we consider Lévy searchers, one must first determine what Lévy parameter is expected to optimize patch detection. Then, recruiting foragers must optimize their search for conspecifics by assuming all other foragers search optimally. As in this setting we consider patches (not resources) to be effectively and approximately uniformly distributed (please find the discussion in Chapter 4), it is known that ballistic searches are most efficient (see the discussion in Section 1.3.1.1). Additionally, it is critical to note that, as patches are ephemeral, recruitment of conspecifics either needs to be fast, or it needs to occur in such a way that recruiting events are not far from the patch. We assume that the latter is both more attainable and important, and as such recruiting foragers should not move far away from the patch to which others are to be recruited. Hence, as optimal searches for patches are ballistic searches, optimal recruitment that maximizes conspecific encounter rates are optimized when recruiters search locally, i.e.:

Hypothesis 3.2. *When recruiting conspecifics, encounter rates are maximized when diffusion characteristics of the recruiter contrast with those of conspecifics.*

As the goal of the recruiter is to encounter (and subsequently recruit) conspecifics while remaining close to the patch, one can imagine a more passive recruitment scheme where the recruiting forager remains on the patch to be more effective. Interestingly, such a passive scheme reduces the system to a group forager system where foragers join successful others (as discussed in Section 1.4.1). However, benefits of such a passive scheme depend strongly on forager densities and interaction ranges. When effective forager densities are high, encountering conspecifics is not difficult, and thus passive recruitment might be advantageous. Note that effective forager density contains interaction ranges as well, as large interaction ranges additionally alleviate the need for more intricate recruiting searches, resembling strategies closely related to broadcasting [106, 309, 310]. This leads us to the following hypothesis:

Hypothesis 3.3. *Active recruitment results in higher collective foraging efficiencies than passive recruitment, but only when effective forager densities are low.*

□

As we discussed in Section 1.5, in natural systems foragers can die and reproduce, thus generating intricate population dynamics that depend strongly on foraging behavior and habitat characteristics [311]. Most importantly, effective loss of habitat is currently a major threat to the stability of populations [77], resulting in a rapid decline of biodiversity [248].

A prominent effect of habitat loss is increased habitat fragmentation [79], where patches (fragments) become smaller and more spatially separated [87, 88]. Whereas habitat often facilitates resource growth, and as foraging behavior depends strongly on resource (thus habitat) availability, we argue that optimal foraging strategies should extend from individual or groups of foragers to populations of foragers. This leads to the following research question:

Research question 4 (Chapter 5). *How does landscape fragmentation influence populations of optimal foragers and how can optimal foraging responses lead to changes in spatial configurations affect the landscape?*

To this end, we would like to model population dynamics on fragmented landscapes. Introduced in Section 1.5.1.1, spatial characteristics can be captured by discussing lattices wherein each site can impart a specific influence on populations residing on that site. For example, within the context of fragmentation only on sites belonging to the spatially separated fragments (patches) experience organisms positive reproduction rates. As a result, reproduction can *only* occur on patches. Moreover, lattices enable the modeling of fragmented landscapes using neutral landscape models (NLMs). In brief, NLMs were introduced as to model these patterns without full understanding of the underlying processes that generate them [312–315]. In general, these models produce lattices that can approximate fragmented landscapes and can therefore be combined with population models to unveil how fragmentation influences population dynamics (see e.g., [238]).

More specifically, we develop a stochastic predator-prey (forager-resource) model on a fragmented lattice wherein we vary predator dispersal and the degree of fragmentation. Consistent with OFT, we let predators forage (i.e. disperse) according to a Lévy walk, while prey are sessile. Demographic fluctuations are mediated by having prey reproduce onto adjacent eligible sites, i.e. sites that are both empty and belonging to a habitat fragment. Prey can be consumed by predators, which can trigger a predator reproduction event onto the site belonging to the prey, hence restricting predator reproduction to the fragments as well. Then, we employ a Monte Carlo approach, by randomly choosing sites and updating them according to the demographic rules.

As prey consumption within this model effectively represents destructive foraging, the rate of consumption strongly defines the stability of both populations. In turn, the rate of consumption is influenced heavily by foraging behavior, which determines specific predator dispersal rates [238]. Low dispersal rates result in overconsumption of prey as predators are locally bound. In contrast, high dispersal rates result in underconsumption as predators spend most of their lives traveling in between patches, instead of feeding and reproducing on them. As a result, intermediate dispersal rates are expected to maximize population densities, however its precise

level determines on the specific degree of fragmentation within the habitat. As fragmentation effects become more pronounced, patches become smaller on average, and thus local demographic fluctuations can result in local extinction [316, 317], negatively affecting population densities. However, when predators are highly dispersive, these effects might not be detrimental as patch encounters are unlikely to be followed by overconsumption and subsequently local extinction. Therefore, we pose the following hypothesis:

Hypothesis 4.1. *Strong fragmentation negatively impacts population densities, but its severity depends strongly on predator dispersal rates.*

Notably, changes in demographic rates, such as increased reproduction rates (e.g., through evolution), most often occur on much longer times scales than those on which the current habitat changes take place. In contrast, adaptations in foraging strategy, corresponding to changes in predator dispersal, can occur rapidly [40, 136, 139]. Therefore, one would expect predators to respond optimally to the specific degree of fragmentation. However, from a more evolutionary standpoint, it is not precisely clear what incentive predators optimize for. While intuitively one would assume predators to optimize for predator densities, population stability might instead pressure predators to optimize for ecosystem health. To assess this, we introduce *species richness* as a metric that captures the relative occurrence of predator and prey, under the assumption that healthy ecosystems exhibit equal abundance of species [318, 319]. As predators, not prey, mediate rapid changes within the environment through adopting optimal dispersal rates, we state the following hypothesis:

Hypothesis 4.2. *Species richness is largely mediated by predator densities and subsequently depends strongly on predator dispersal rates and the degree of fragmentation.*

Critically, as prey are sessile, habitat regeneration can only occur when it is physically connected to sites whereon prey live. In other words, spaces between fragments act as barriers that prey cannot cross [320, 321]. As a result, disconnected patches that have become void of prey due to local overconsumption through predation, will never be inhabited by prey again. As a result, our model suggests that irreversible habitat loss occurs in disconnected landscapes. Moreover, as smaller patches are more prone to local extinction events [322], we conclude with the following hypothesis:

Hypothesis 4.3. *Fragmented environments undergo irreversible loss of habitat, even when predator respond optimally as to maximize species richness. This habitat loss is largely manifested by depletion of small patches.*

□

1.8 Dissertation outline

Within this dissertation, we would like to emphasize that each chapter corresponds to work that is published in international journals, or has been submitted for publication³. The research that will be discussed pertains to foraging over different spatial and temporal scales, ranging from individual foragers with high individual complexity to entire populations of foragers. In general, the work aims to answer the posed research questions and test the corresponding hypotheses.

To this end, we shall first study an individual forager in Chapter 2, and study the influence of a learned spatial memory of the foraging efficiency using an agent-based model. When the forager is highly certain that its model is correct, it is more likely to exploit this model by sampling goal states when it has not detected a resource recently. We shall show that spatial memory increases foraging efficiency by exploitation of known resource locations when foraging non-destructively. However, we also show that this continuous exploitation leads to poor exploration, and thereby frequent memory usage negatively affects patch diversity. Despite this, our memory model can be easily adapted to account for different types of resources if those are necessary for the survival of the forager.

While memory is known to be only beneficial in predictable environments, we study destructive foraging by a group of foragers competing for resources in Chapter 3. In particular, we study systems wherein foragers execute intermittent random searches that interchange highly diffusive, extensive searches with localized, intensive searches and informed searches guided by attraction towards (recently) successful conspecifics. More specifically, in this chapter we focus on attaining a quantitative description of the impact of resource fractility and joining ranges on the foraging efficiency. We determine both the foraging efficiency at the individual and at the group level. Interestingly, the conditions under which group advantages are highest are precisely those where individual advantages are lowest. In more detail, joining others is beneficial at the group level only when resources are sufficiently clustered and group sizes are small and joining ranges are not too large. In contrast, individual advantages, expressed as a reduced variation in resource intake rates, are largest when resources are not clustered, or when group sizes are large and joining ranges small. As a result, this chapter highlights that when individuals within a group act with selfish intent, group-level incentives, such as high foraging efficiencies, might not be attained at the expense of individual benefit.

In Chapter 4, we replace competition by cooperation and study a col-

³Effectively, it means that each chapter is self-contained. Note that some of the text and figures might have been changed to accommodate the reader of this dissertation.

⁴Note that although resources are not destroyed upon detection, patch ephemerality here approximates destructive foraging. See Chapter 4 for more details.

Table T.1.1: Structured overview of work presented in this dissertation.

Chapter	2	3	4	5
Research question	1	2	3	4
Environment	clumped, static	fractal, dynamic	clumped, ephemeral	fragmented, dynamic
Foraging type	non- destructive	destructive	destructive ⁴	destructive
Interactions	-	competitive	collective	population

lective foraging system. We examine how both the resource distribution and forager density affects the foraging efficiency of the collective. Within an agent-based model setting, we model patch ephemerality by having patches rich in resources disappear after some time. Cooperation between foragers is introduced by having individuals recruit others towards the patch with some probability that depends on the quality of the patch. Recruitment is realized by having the recruiter that initially detected the patch, actively search for others, and informing them about the location of the patch. Encountered foragers are then recruited and travel towards the patch as to feed on its resources. Since the system is collective, we study foraging efficiency on the group level, and show that patch ephemerality and availability highly influence the benefits of this altruistic recruitment behavior. More specifically, we show that recruitment is only beneficial when patches are both scarce and persistent. Moreover, when comparing active recruitment with a more passive strategy, we show that the advantage of active recruitment depends on both forager density and the interaction range. In general, we find that active recruitment is more beneficial when forager densities are low and interaction ranges are short.

As resource distribution characteristics heavily determine foraging strategies, we ask how species survival and landscape fragmentation interact in Chapter 5. By precisely controlling the degree of fragmentation and forager movement in a predator-prey system with sessile prey, we show that optimal forager dispersal rates strongly affect population stability in fragmented ecosystems. When the environment expresses little fragmentation, our results indicate that high dispersal rates maximize population densities, while low dispersal rates result in near extinction. Effectively, high dispersal rates correspond to systems of highly diffusive foragers that quickly locate large patches, while not overexploiting them as they are prone to leave patches as well. Optimal dispersal rates decrease as fragmentation increases, since highly diffusive foragers are much more likely to miss the small fragments on which their prey is located. Additionally, our results predict habitat loss resulting from local prey extinctions. This loss of habitat is irreversible, as prey populations cannot recover the depleted patches since they are disconnected and separated by impenetrable

barriers. Habitat loss is subsequently followed by decreases in population densities and we show that these effects are more pronounced in highly fragmented systems. Most importantly, we show that these negative effects are significant even when foragers adopt strategies that maximize species richness. However, our results indicate that habitat loss can be reduced, but not prevented, when foragers adopt optimal foraging behavior, highlighting the important role of foraging behavior in ecosystem stability.

Finally, the dissertation is concluded in Chapter 6, gaps in the presented research are discussed and an outlook is presented. As to facilitate the reader, an overview of the chapters, what type of system is studied and what research questions they address is provided in Table T.1.1.

1.9 List of publications

The work presented in this dissertation is published in, or submitted to, international scientific journals. The list below contains research that is not discussed in this dissertation, but which has been published in international scientific journals or presented at international conferences.

1.9.1 Publications in international journals (as listed in the Science Citation Index ⁵)

1. **Johannes Nauta**, Yara Khaluf, Pieter Simoens, Ricardo Martinez-Garcia (in review) *“Foraging behavior and patch size distribution jointly determine population dynamics in fragmented landscapes”*. Journal of the Royal Society Interface
2. **Johannes Nauta**, Pieter Simoens, Yara Khaluf (2021) *“Group size and resource fractality drive multimodal search strategies: a quantitative analysis on group foraging”*. Physica A - Statistical Mechanics and its Applications
3. **Johannes Nauta**, Yara Khaluf, Pieter Simoens (2021) *“Resource ephemerality influences effectiveness of altruistic behavior in collective foraging”*. Swarm Intelligence
4. **Johannes Nauta**, Yara Khaluf, Pieter Simoens (2020) *“Hybrid foraging in patchy environments using spatial memory”*. Journal of the Royal Society Interface, 17 (266), pp. 20200026
5. **Johannes Nauta**, Christof Mahieu, Christophe Michiels, Femke Ongenae, Femke De Backere, Filip De Turck, Yara Khaluf, Pieter Simoens (2019) *“Pro-active positioning of a social robot intervening upon behavioral disturbances of persons with dementia in a smart nursing home”*. Cognitive Systems Research 57, pp. 160-174

1.9.2 Publications in international conferences (as listed in the Conference Proceedings Citation Index ⁶)

1. **Johannes Nauta**, Stef van Havermaet, Pieter Simoens, Yara Khaluf (2020) *“Enhanced foraging in robot swarms using collective Lévy walks”*. ECAI2020, the 24th European Conference on Artificial Intelligence, pp.171-178

⁵These publications are classified as ‘A1’ by Ghent University according to the [following definition](#): “Articles included in one of the ISI Web of Science indexes ‘Science Citation Index’, ‘Social Science Citation Index’ or ‘Arts and Humanities Citation Index’. Limited to the publications document type: article, review, letter, note, proceedings paper.”

⁶These publications are classified as ‘P1’ by Ghent University according to the [following definition](#): “Proceedings included in one of these ISI Web of Science indexes: ‘Conference Proceedings Citation Index - Science’ or ‘Conference Proceedings Citation Index - Social Science and Humanities’. Limited to publications document type: article, review, letter, note, proceedings paper, with exception of publications classified A1.”

2. Ozan Çatal, Tim Verbelen, **Johannes Nauta**, Cedric de Boom, Bart Dhoedt (2020) “*Learning perception and planning with deep active inference*”. ICASSP 2020, IEEE International Conference on Acoustics, Speech and Signal Processing, pp. 3952-3956
3. Ozan Çatal, **Johannes Nauta**, Tim Verbelen, Pieter Simoens, Bart Dhoedt (2019) “*Bayesian policy selection using active inference*”. Workshop on “Structure & Priors in Reinforcement Learning” at ICLR 2019, Seventh International Conference on Learning Representations.

1.9.3 Publications in international conferences (as listed in proceedings of academic conferences⁷)

1. **Johannes Nauta**, Pieter Simoens, Yara Khaluf (2020) “*Memory induced aggregation in collective foraging*”. ANTS2020, The 13th International Conference on Swarm Intelligence, pp. 176-189
2. Ilja Rausch, **Johannes Nauta**, Pieter Simoens, Yara Khaluf (2020) “*Modeling the influence of social feedback on altruism using multi-agent systems*”. ALIFE2020, the 2020 Conference on Artificial Life, (Vol. 325), pp. 727-735
3. **Johannes Nauta**, Yara Khaluf, Pieter Simoens (2019) “*Using the Ornstein-Uhlenbeck process for random exploration*”. 4th International Conference on Complexity, Future Information Systems and Risk (COMPLEXIS2019), pp. 59-66

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⁷These publications are classified as ‘C1’ by Ghent University according to the [following definition](#): “Articles published in proceedings of academic conferences, not included in ‘A1’ or ‘P1’ (full articles with exception of abstracts, unpublished presentations, posters, ...)”

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2

Hybrid foraging in patchy environments using spatial memory

Abstract

Efficient random searches are essential to the survival of foragers searching for sparsely distributed resources. As resources are distributed within patches, spatial memory over the detected resources can be beneficial towards optimizing the search efficiency. However, because foragers have limited memory, storing each resource location separately is unrealistic. Therefore, in this chapter we propose a scheme for learning a spatial distribution over resource locations instead. We demonstrate that an ensemble of Gaussian mixture models is a suitable candidate for such a memory component. We propose a hybrid foraging strategy wherein a forager interchanges random Lévy searches with informed movement to locations sampled from memory. Our results show that frequent memory usage leads to increases in search efficiencies by continuous revisitation of non-destructive resources. However, this negatively affects both the resource and patch diversity, indicating that frequent memory usage does not necessarily optimize multi-objective searches. Hence, our results suggest that benefits of memory should depend on the specific incentives of the forager. Furthermore, analysis of the distribution over walking distances of the forager reveals that memory changes the underlying walk characteristics. Specifically, the forager resorts to Brownian motion instead of Lévy walks, due to memory effects resulting in the truncation of the long, straight line displacements. Therefore, the results in this chapter indicate that memory greatly affects forager dispersal characteristics and that foragers need to carefully balance exploration and exploitation for their foraging behavior to be efficient.

2.1 Introduction

Searching for resources whose distribution is unknown is an important problem in behavioral ecology. Locating scarce food sources is fundamental for the survival of the forager, and hence optimal foraging strategies must be employed in order to maximize survival probability [2, 3]. Random searches can optimize the search for sparsely distributed resources [4–8], however including memory effects that change the random search into an informed search can highly influence the search efficiency of the forager [9–11]. While random searches are a necessary component of any search strategy, its importance decays over time if the forager has the capacity to remember where resources are located. If all resource locations are known, the random nature of the search can be completely ignored in favour of purely informed movement [12, 13]. Thus, a trade-off between exploration (based on a non-informed random search) and exploitation (based on the gathered information) naturally arises when the resource encounter rate is to be optimized through means other than random searches. This work proposes a hybrid foraging strategy based on memory, wherein random search and informed motion are alternated.

Although informed movement seems to enable further optimization of the search efficiency, any potential memory component still relies heavily on the efficiency of random searches for resource localization. In particular, Lévy walks have been shown to optimize random searches in environments wherein the resource distribution is sparse [2, 4, 5, 8, 10, 14], even in cases where resources were moving [15]. While search optimality of Lévy walks has been observed when resources are sparsely distributed, real-world environments are often both sparse and patchy [16–19], illustrating scale-free, fractal-like patterns [20–22]. These environments consist of patches containing densely distributed resources and interpatch regions where no resources are located (see Fig. 2.1). Nonetheless, Lévy walks have been found to be robust to such fragmentation effects [10, 23]. Moreover, Lévy walks have been found to encompass strategies which optimize patch diversity, wherein multiple-objectives play a key role in the random search process [14].

Patchy distributions within real-world environments remarkably alleviate the necessity for the foragers cognitive abilities to remember the exact positions of resources. Specifically, in this chapter, we show that a forager can estimate patch locations (and thus the resource locations) by learning a spatial distribution over detected resources. Furthermore, by sampling from the learned distribution, the forager can switch to informed movement in cases where no resources have been detected for some time. Hence, a hybrid foraging strategy emerges, in which random searches are alternated with bouts of informed motion. This improves resource visitation rates by visiting regions which are known (or assumed by the model) to contain a high number of resources.

Spatial memory is less beneficial when foraging becomes destructive, meaning that resources are destroyed (e.g. consumed) upon detection. Obviously, learning a spatial distribution over resource locations that constantly changes due to destructive foraging is futile, since past locations of resource detection do not convey any information about future locations. Additionally, when the resources are constantly moving, for example in predator-prey systems¹, advantages of memory disappear. As expected, memory has been found to be more advantageous in predictable environments [24]. It is important to note that natural resources have the tendency to regenerate periodically, and hence a forager can, in principle, exploit knowledge of the regeneration times in order to return to patches rich in resources, e.g. seasonal changes. Such behavior has been observed in Capuchin monkeys, which couple spatial locations to known (or learned) time-varying patch qualities [25]. Stochastic regeneration rates are another type of regeneration observed in nature, for example the nectar in flowers [26], making learning the time dependence on the patch quality more difficult. While these types of interplay between resource regeneration and destructive foraging may correspond to more realistic searches, e.g. when describing foraging behavior of marine predators that consume their resources [27], the empirically determined optimal Lévy parameter was often close to the non-destructive optimum. Moreover, in ecology, patches are often dense [28], meaning that destructive foraging can effectively be approximated by non-destructive foraging behavior since resources are within close proximity of another. This suggests that the consumption rate of such predators might be low enough, or that the regeneration rate within the patch is high enough, such that their foraging can be approximated as non-destructive. Hence, in the remainder of this study we limit ourselves to non-destructive foraging tasks in static environments. Destructive foraging, foraging with known periodic or stochastic regeneration rates, and foraging for dynamic resources are topics for future research.

Next, we ask what features a good memory component for a forager in a patchy environment should have. An example of a simple random search that employs an infinite memory kernel is the extensively studied self-avoiding random walk. However, such models fail to capture memory effects that are useful for maximizing resource visitation, since in non-destructive searches revisitation of resources is a very efficient foraging strategy. Other memory models that have been studied consist of the general direction wherein the forager prefers to move [29], location of a previously detected resource [30, 31] or a number of resources detected within the last set of steps [10]. However, more intricate memory models have been discussed based on diffusion models with drift vectors pointing towards patches with high resource densities [11, 32]. In general, these works

¹In such systems, foragers are the predators, while resources are the prey. See also Chapter 5.

all indicate that memory is beneficial for maximizing resource visitations, given that the foraging is non-destructive, regardless of the specific choice of memory model. Interestingly, (time-varying) spatial memory has been experimentally verified in Capuchin monkeys [25, 33, 34]. These results suggest that intelligent foragers are capable of maintaining a more complex memory model that is able to estimate distributions over resources. Therefore, such a model shall be introduced below.

In this chapter, we employ a Gaussian mixture model (GMM) that acts as the memory component, since it fits all requirements of a spatial memory. Due to their universal approximation properties [35, 36], they can be used to learn a spatial resource distribution over patchy landscapes from which the forager can sample goal locations. An additional advantage of a mixture of Gaussians, is that each component can be weighted differently. This enables differentiating different patches, for example based on attributes of the patch, e.g. nutritional value. Furthermore, GMMs can be learned incrementally [37, 38], allowing a forager with limited memory capacity to store positional resource information within a small number of parameters that define the mixture model. Aside from real-world foragers not having infinite memory capabilities, a major advantage is that such incremental learning procedures can easily adapt to possible changes in the resource distribution. Furthermore, instead of learning a single GMM, we propose incremental learning of an ensemble of GMMs as to account for a model disagreement that measures the foragers' certainty of the learned distribution. This allows the foragers to make decisions based on the estimated correctness of their memory model [39–41]. More specifically, we let the truncation of the random search component of the emerging hybrid walk be more likely when the forager is certain of its learned distribution over resources. We believe that the results presented in this chapter are beneficial towards understanding the influence of memory in foraging in patchy environments.

The remainder of this chapter is organized as follows. In Section 2.2 we describe the patchy environment setup and discuss the random search and the learning of the spatial distribution. In Section 2.4 we present the results of numerical simulations and discuss several properties of the resulting random search with informed movement. Finally, in Section 2.5, we conclude the chapter and additionally present remarks and a future outlook on further experiments.

2.2 Model description

We start by specifying the informed search characteristics, which contains both a random search and a memory component. The forager alternates between the two components through truncation of the random search based on the learned memory model. Such a hybrid foraging strategy shows similarity with previously studied composite or adaptive Lévy

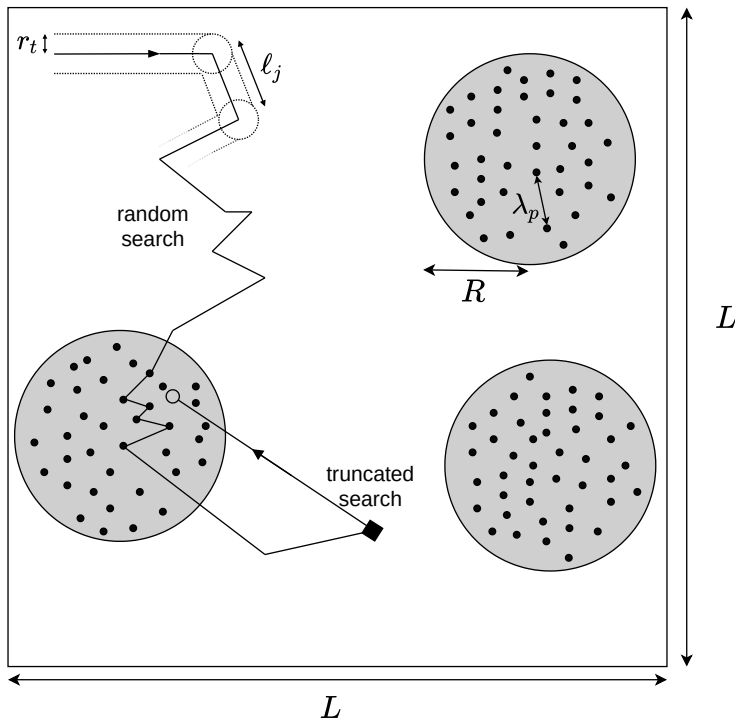


Figure 2.1: Illustrative example of the environment and the memory model for $N_p = 3$ patches with radius R and intrapatch mean free path λ_p . Resources (black dots) are distributed homogeneously (uniformly) within the patches and each patch contains an equal amount of resources n_p . The random search is truncated (black square) according to the truncation probability (Eq. (2.2)) and, as a result, the forager moves towards a sampled goal (open circle). After the informed motion, the random search continues with the forager now (back) in the dense patch.

walks [42–44], however in this work the change in strategy originates from the memory component of the informed search.

2.2.1 Description of the informed search

Let us first discuss the random search component of the informed search. The random search is realized by assuming that foragers execute a Lévy random walk. Foragers following a Lévy walk pattern have their displacement lengths distributed according to a (truncated) power law $p(\ell) \sim \ell^{-\alpha}$, for $\ell_0 < \ell < L$ and where $1 < \alpha \leq 3$ is called the Lévy parameter. Note that $\alpha \leq 1$ corresponds to non-normalizable distributions. For $L \rightarrow \infty$ this power law distribution of displacement lengths has the same asymptotic behavior as the family of Lévy stable distributions [7, 45], meaning

that higher order moments are infinite. However, in the real world such moments can never be infinite, since they correspond to infinitely large displacements. Therefore, we employ a truncated power law distribution

$$p(\ell) = \begin{cases} \frac{\ell_0^{\alpha-1}}{(\ell_0^{1-\alpha} - L^{1-\alpha})} \ell^{-\alpha} & \text{if } \ell_0 < \ell \leq L, \\ 0 & \text{otherwise,} \end{cases} \quad (2.1)$$

that effectively truncates walk distances at the environment size L . Here, ℓ_0 is the minimum displacement, hence omitting steps of a much smaller scale that is irrelevant to the search process [46]. It is important to note convergence of the truncated power law of Eq. (2.1) is ultraslow, meaning that the general characteristics of Lévy distributions are conserved during foraging [47].

In the asymptotic limit, the Lévy parameter defines the diffusion characteristics of the random walk, being anomalous (superdiffusive) for $1 < \alpha \leq 3$ and normal (Brownian) for $\alpha \geq 3$ [48]. When $\alpha \rightarrow 1$, the forager moves ballistically, i.e. only straight line motion is visible. For intermediate values, the random walk displays scale-free characteristics with statistically relevant large jumps that govern the diffusive capabilities of the forager. Such Lévy walks have been found to be optimal over a wide range of resource distributions [23]. When foraging is non-destructive, $\alpha_{opt} \approx 2$ has been found to optimize the Lévy random search. In destructive foraging, ballistic motion with $\alpha_{opt} \rightarrow 1$ emerges as the optimal strategy. Intermediate searches, e.g. setting a degree of resource revisitability through regeneration [49, 50], give rise to intermediate values $1 \leq \alpha_{opt} \leq 2$ that optimize the random search. Additionally, values of $2 \leq \alpha_{opt} \leq 3$ can be found when a bias (e.g. an external drift, such as a current) is present [51]. For a more extensive overview of Lévy random searches, we refer the interested reader to previous works on Lévy walks in a foraging setting [7, 28].

The actual informed search alternates the Lévy random search with memory induced motion, wherein the forager steers towards a goal location sampled from its memory. Foragers execute a Lévy random search that is truncated based on the learned model. Every j th step adheres to the following rules:

- (a) Draw a walk distance ℓ_j from the (truncated) power law distribution $p(\ell) \sim \ell^{-\alpha}$ (Eq. (2.1)), and an orientation angle θ sampled uniformly between 0 and 2π , and walk along the sampled path with fixed steps of size ℓ_0 .
- (b) While traveling the distance ℓ_j with steps of size ℓ_0 , the forager scans its direct environment within a radius r_t after each step. When a resource is detected, the current walk is truncated. The forager moves to the resource location² and stores the resource location in its tempo-

²In our study, the perception radius is of equal size as the step size of the forager, trivializ-

- rary (limited) memory. After detection of a resource, a new walking distance and angle are sampled according to (a).
- (c) After each step, when no resource is detected, the forager truncates the random search according to the number of steps L_0 wherein no resource was encountered, a model disagreement φ (see Section 2.2.3) and a truncation parameter β (see below).

$$p(L_0, \varphi) = 1 - \exp\left(-\frac{\beta L_0}{\varphi}\right). \quad (2.2)$$

After the search has been truncated, the forager resorts to exploitation by sampling a goal state from its model $q_E(\mathbf{x}, \Theta)$ (see Eq. (2.3))

$$\mathbf{x}_{goal} \sim q_E(\mathbf{x}|\Theta),$$

where Θ are the parameters of the learned spatial distribution. The forager then moves towards the sampled goal state, again with steps of fixed size ℓ_0 . After this informed motion is finished, the forager starts the random search again at (a).

We fix the step size to the detection radius in Eq. (2.1), i.e. $l_0 = r_t$, hence naturally omitting steps smaller than the detection radius, as those are meaningless within a search context. Additionally, the upper truncation at L corresponds to the limit scale of the environment. Hence, the range $r_t < \ell \leq L$ appropriately defines the relevant scales of the search process.

First, let us discuss the truncation of the random search in more detail. Specifically, we adapt the framework of Zhao *et al.* [8] by including the model disagreement φ in the random search truncation probability of Eq. (2.2). This is indicated by the rule that *the longer the forager has traveled and the lower the model disagreement, the more likely the forager is to truncate its random search and exploit its knowledge*. The truncation parameter β defines the foragers' behavior (see Fig. 2.2 for an illustrative example). Low values of β correspond to *naive* foragers, which require an extremely low model disagreement before they trust their model enough to sample goal states from. This results in the forager relying on exploration, hence the random search will be the main component that determines the search efficiency. In contrast, relatively large values of β correspond to *greedy* foragers, that quickly resort to only sampling goal states from their model, even though their model might have a large disagreement and thus likely fails to describe the true resource distribution. In between these two modes, there exists an *intermediate* forager that balances exploration and exploitation and hence is expected to optimize the search for resources. The truncation parameter β is thus an important metric that defines the behavior of the forager.

ing the process of the forager moving to the resource location. However, when the perception radius is much larger than the step size, the forager should compute a relative angle between itself and the detected resource and travel in that direction until it is on the resource.

The memory induced informed movement after truncation of the random search is defined by taking steps along a calculated difference vector between the current position and the goal, again with steps of size $\ell_0 = r_t$. Thus, after the informed movement has finished, the agent is within a detection radius r_t of the sampled goal state x_{goal} . If the model is correct (i.e. it correctly models the sparse and patchy resource distribution), each goal position corresponds to a position within a patch, and thus each goal state is, in principle, close to a (previously detected) resource. However, when the model is incorrect this does not have to be true. During the informed movement, the forager continues to detect resources and truncates the informed motion once a resource has been detected. This results in a more natural search, since in real scenarios it is unlikely that foragers will skip over available resources in favour of some arbitrary goal, given that we assume patches with the same attributes.

The resource detection is based on a model of an effectively blind forager, that only encounters resources within its perception range r_t [6]. While it can be argued whether animals capable of learning a spatial map have a limited perception radius, empirical results indicate that even with memory (perhaps even due to memory), animals display superdiffusive random searches when foraging [30, 52]. Furthermore, as the sparsity is expressed in terms of the detection radius, increases of the detection radius do not change the outcome of the numerical experiments, but simply changes the scale of the underlying foraging process. While many animals have evolved intricate perception methods, these are simply there to decrease the intrapatch resource density λ_p and hence such situations will be captured by discussing low values of the mean free path, which we do in Section 2.4.

Note that the truncation based on the model is sure to decrease the diffusivity of the resulting walk. In other words, the informed search might not carry the same diffusion characteristics of the free Lévy walk, which shows superdiffusive scaling behavior. Depending on the resource density, a switch to less diffusive searches might be realized by the forager, due to the searches revisiting a small set of resources within a patch with high resource density, compliant with empirical data [30, 34]. We both measure the characteristics of the resulting motion as well as introduce different search efficiency metrics in order to investigate the informed search in more detail.

2.2.2 Incremental learning procedure for spatial memory

In order to learn a spatial distribution over resource locations, we employ incremental learning of a GMM with a variable number of mixture components. The variety in the number of components equips foragers with the ability to not overfit on the stored resource locations, when a simpler model would suffice. Further, we argue that the decision of the forager, e.g.

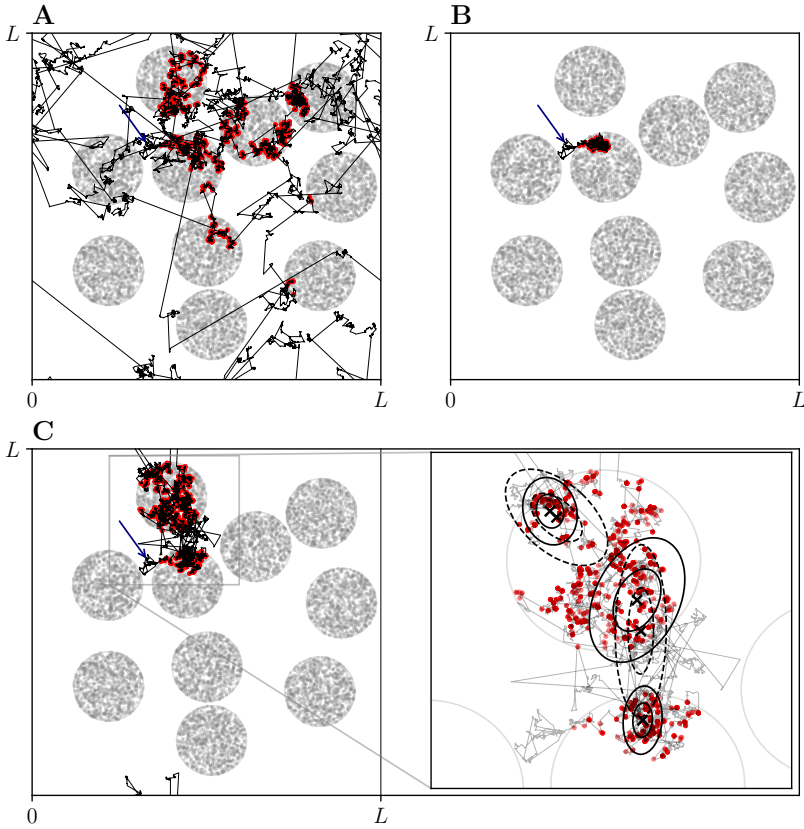


Figure 2.2: Examples of informed search for different truncation parameters β , where the task is to find $2 \cdot 10^3$ resources. Red dots indicate detected resources while the black lines are the trajectory of the forager. Patches and resources within the patches are denoted by the gray circles and dots respectively. The arrow indicates the (identical) starting position of the forager. (A) $\beta = 10^{-9}$: Naive forager that never employs a model, but continuously explores the environment using its random search. (B) $\beta = 10^{-1}$: Greedy forager that almost always uses its model and hence quickly fixates around the first detected resources. (C) $\beta = 10^{-5}$: Intermediate forager that balances exploration and exploitation to generate a model over several patches. The zoomed in region contains more detail on the visited region and includes continuous and dotted ellipses that represent variances of the components of the Gaussian mixtures of two ensemble members ($K = 2$), while crosses indicate the means.

the time at which to execute informed movement versus a random search, should be depending on the memory model. Hence, the GMM should be able to reflect some type of ‘certainty’ that determines the foragers’ belief that the model is accurate. If the model is indeed accurate, the forager

should rely less on random search due to informed motion being the superior alternative. While a single GMM intrinsically captures the likelihood of the data given the model, ascribing ‘certainty’ to the model gives rise to an arbitrary threshold value that is hard to determine. Instead, we deploy the foragers with an ensemble of GMMs from which the disagreement between each member of the ensemble and the full ensemble is able to reflect the model uncertainty [39–41]. Thus, the spatial distribution is given by an ensemble of K GMMs, each with M_k components (Gaussians):

$$q_E(\mathbf{x}|\Theta) = \sum_{k=1}^K W_k q_k(\mathbf{x}|\Theta^{(k)}), \quad (2.3)$$

$$\text{with } q_k(\mathbf{x}|\Theta^{(k)}) = \sum_{j=1}^{M_k} w_j^{(k)} \mathcal{N}(\boldsymbol{\mu}_j^{(k)}, \boldsymbol{\Sigma}_j^{(k)}), \quad (2.4)$$

where

$$\Theta^{(k)} = \nabla \times \left(w_1^{(k)}, \boldsymbol{\mu}_1^{(k)}, \boldsymbol{\Sigma}_1^{(k)} \right), \dots, \left(w_{M_k}^{(k)}, \boldsymbol{\mu}_{M_k}^{(k)}, \boldsymbol{\Sigma}_{M_k}^{(k)} \right)$$

the parameters of the k th mixture model within the ensemble, $w_j^{(k)}$ the normalized weights, of each multivariate Gaussian with mean $\boldsymbol{\mu}_j^{(k)}$ and covariance $\boldsymbol{\Sigma}_j^{(k)}$, and W_k the normalized ensemble weights. The normalization of the (ensemble) weights means that $\sum_j w_j^{(k)} = 1$ and $\sum_k W_k = 1$.

We assume that foragers have limited memory, hence each forager incrementally learns the GMM [38]. While the forager explores the environment and detects resources, it stores resource locations in its memory up to a fixed maximum number N_{mem} . When the random search is truncated, the GMM is incrementally updated with the latest N_{mem} detected resources. Next, the resource locations are divided equally over the number of ensemble members K . It should be noted that a minimum number of data points is needed for the ensemble to be trained. Furthermore, GMMs are not suited to be computed over a single data point, hence we need at least a multiple of the total number of Gaussians as the minimum size of the data set. After distribution of the data among the ensemble members, each member learns a new GMM over its subset of the recently detected N_{mem} resource locations, with the number of mixture components between M_{min} and M_{max} . In other words, for each $M \in \{M_{\text{min}}, \dots, M_{\text{max}}\}$ a new GMM is learned. Then, compliant with existing statistical measures, the GMM with the lowest Bayesian information criterion (BIC) is selected as the new GMM [38]. Additionally, the weights of the new GMM are scaled by a forgetting factor f ($0 < f < 1$), which defines how much importance is attributed to the new, incoming data. Values $f \rightarrow 0$ indicate conservative foragers, which do not change their model with new incoming data, while $f \rightarrow 1$ represents progressive foragers that dispose of the current model in favour of the new one. Note that the forgetting factor additionally ensures

normalization of the weights. Next, the previous GMM and the new GMM are joined to form the incrementally updated GMM. However, if the sum of components of the updated GMM exceeds the set maximum M_{\max} , Gaussian components are merged. Which components are merged depends on their similarity, expressed in a symmetric KL divergence

$$D_{\text{KL}}^{\text{sym}} = \frac{1}{2} (D_{\text{KL}}(g_1, g_2) + D_{\text{KL}}(g_2, g_1)), \quad (2.5)$$

where $D_{\text{KL}}(g_i, g_j)$ the KL-divergence between two Gaussians $g_i \sim \mathcal{N}(\boldsymbol{\mu}_i, \boldsymbol{\Sigma}_i)$, given by

$$D_{\text{KL}}(g_i, g_j) = \log \left(\frac{\det \boldsymbol{\Sigma}_j}{\det \boldsymbol{\Sigma}_i} \right) + \text{Tr} \left(\boldsymbol{\Sigma}_j^{-1} \boldsymbol{\Sigma}_i \right) + \left(\boldsymbol{\mu}_j - \boldsymbol{\mu}_i \right)^T \boldsymbol{\Sigma}_i^{-1} \left(\boldsymbol{\mu}_j - \boldsymbol{\mu}_i \right) - D, \quad (2.6)$$

where D is the number of dimensions of the Gaussian and $\det(A)$ the determinant and $\text{Tr}(A)$ the trace of a matrix A . Components that carry the lowest values of the symmetric KL divergence are merged, i.e. components that are most similar, until the total number of components is equal to X_{\max} . Merging two Gaussians is defined by the following set of equations [37, 38]

$$w^* = w_1 + w_2 \quad (2.7)$$

$$\boldsymbol{\mu}^* = \frac{w_1 \boldsymbol{\mu}_1 + w_2 \boldsymbol{\mu}_2}{w_1 + w_2} \quad (2.8)$$

$$\boldsymbol{\Sigma}^* = \frac{w_1 \boldsymbol{\Sigma}_1 + w_2 \boldsymbol{\Sigma}_2}{w_1 + w_2} + \frac{w_1 w_2}{(w_1 + w_2)^2} (\boldsymbol{\mu}_1 - \boldsymbol{\mu}_2) (\boldsymbol{\mu}_1 - \boldsymbol{\mu}_2)^T, \quad (2.9)$$

where the asterisk denotes the new Gaussian. The merged Gaussians are deleted from the GMM and replaced by the newly merged Gaussian. An illustrative example of the final result of the learning procedure is depicted in Fig. 2.2(C).

2.2.3 Truncation of the random search

With the spatial distribution in place, the forager needs to decide whether to truncate the current random search in favour of informed motion towards known (estimated) resource locations. To compute the truncation probability of Eq. (2.2), the agent explicitly computes an uncertainty φ over the learned ensemble. This uncertainty, the *model disagreement*, is defined as the KL divergence between each member of the ensemble and the full ensemble distribution

$$\varphi = \frac{1}{K} \sum_{k=1}^K D_{\text{KL}} \left[q_k(\mathbf{x} | \Theta^{(k)}) || q_E(\mathbf{x} | \Theta) \right]. \quad (2.10)$$

Division by the number of ensemble members K ensures that the influence of memory is independent of the number of ensemble members. Since there does not exist a closed form solution for computing the KL-divergence between (ensemble) mixtures of Gaussians, like there is for two Gaussians in Eq. (2.6), we resort to Monte Carlo approximation [53], where

$$D_{\text{KL}} [q_k || q_E] \approx D_{\text{MC}} [q_k || q_E] = \frac{1}{N} \sum_{i=1}^N \log \frac{q_k(\mathbf{x}_i | \Theta^{(k)})}{q_E(\mathbf{x}_i | \Theta)}, \quad (2.11)$$

with $\mathbf{x}_i \sim q_k(\mathbf{x}_i | \Theta^{(k)})$ samples from ensemble member k . Note that even though the result is only exact in cases where $N \rightarrow \infty$, the forager does not require high accuracy of the integral, since it is not interested in the precision rather the order of magnitude of the disagreement.

2.2.4 Model summary

In summary, hybrid foraging encapsulates both a random search and informed motion based on the memory model. The forager learns an ensemble of GMMs over a dataset of resource positions detected during the random search. From this ensemble, the model disagreement φ is computed, defining the uncertainty the forager has over the distribution of resources. The tuning parameter β determines the truncation probability $p(L_0, \varphi)$, which increases with the number of steps without detecting a resource L_0 . The truncation probability depends on the model disagreement, where high model disagreements result in lower truncation probabilities, hence longer random searches, than when the model disagreement is low, corresponding to more frequent informed motion towards sampled goal resources.

2.3 Methods

2.3.1 Environment description

We consider a two-dimensional (2D) $L \times L$ space with periodic boundaries. The periodic boundary conditions effectively reflect infinite environments, akin to natural habitats being much larger than the forager itself. The forager is able to detect resources within a direct detection radius r_t . The task of the forager is to find a fixed number of resources, i.e. the search is only halted after a specific number of resources have been detected. As an indication of the resource sparsity, the mean free path λ_e can be computed by denoting that the cross-section of the resources equals $2r$ and the density $\rho = N/L^2$ can be expressed in the number of resources N and the area of the environment. The mean free path indicates the average distance between consecutive resources and is given by [4]

$$\lambda_e = (2r_t \rho)^{-1} = \frac{L^2}{2r_t N}. \quad (2.12)$$

Several sparsities can be studied by fixing the values for r and N , and varying λ_e which defines the environment size using Eq. (2.12) [5]. Note that the above expression for λ_e holds in general for any distribution over resources, thus including sparse and patchy distributions, however it is less useful when the environment is patchy (see, e.g., [10]). In those cases, the *intrapatch* mean free path is more appropriate. In patchy environments, the resources are divided over N_p patches, with each patch containing the same number of n_p resources (i.e., $N = N_p n_p$). Then, the intrapatch mean free path λ_p —the mean free path within the patches—can be computed if we consider the patches to be non-overlapping circles with radius $R = wL < L$, $0 \leq w \leq 1$. Then we have

$$\lambda_p = \frac{\pi R^2}{2r_t n_p} = \frac{\pi w^2 L^2}{2r_t n_p}. \quad (2.13)$$

The intrapatch mean free path can be expressed in terms of the mean free path, through combining Eqs. (2.12) and (2.13), giving

$$\lambda_p = \pi w^2 N_p \lambda_e. \quad (2.14)$$

Note that the mean free path and the intrapatch mean free path are indeed equal if the total area of all the distinct patches equals the total area of the environment. This allows us to forego the use of the mean free path λ_e in favor of the intrapatch mean free path λ_p ; the (more) relevant statistic in patchy environments.

In all following experiments, the forager is equipped with the task of finding a minimum of $N = 10^4$ resources. Within the environment, we distribute $n_p = 1000$ resources uniformly within each patch, where the radius of each patch is set to $R = 0.1L$. The total number of patches is set to $N_p = 10$. The size of the environment L is determined by the intrapatch mean free path λ_p , and is computed following Eq. (2.13). The step size, and subsequently the detection radius, is the unit for the system and is hence chosen to be $r_t = 1$. Results are averaged over 500 realizations, unless mentioned otherwise.

2.3.2 Measuring the search efficiency

In random searches, the efficiency of the process is often tightly interconnected with the survival of the forager, e.g. individuals might starve if they do not find enough food [54, 55]. Hence, an appropriate metric that captures the efficiency is necessary. Obviously, one cannot uniquely define a search efficiency metric that captures all possible constraints. Such constraints can vary from minimizing the time in between subsequent resource visits [51] to minimizing energy consumption along the foraging trajectory [54–56].

We define two separate search efficiencies. The first search efficiency η_s defines the rate at which resources are detected. It is defined by

$$\eta_s = \frac{n}{d}, \quad (2.15)$$

where n indicates the total number of resources found and d denotes the total distance traveled by the forager. This definition of the search efficiency has been widely deployed for studying random searches [4–8, 23]. However, as correctly identified in a previous study [14], it fails to capture patch diversity. While the search efficiency of Eq. (3.5) correctly measures the number of resources per traveled distance unit, it does not capture from which patch these resources originated. The result is that revisitation of a single resource, or a few close-by resources within a single patch, greatly increases the search efficiency. We shall see that such behavior occurs when memory effects are strong, and hence the search efficiency that follows the above definition does not reflect more realistic scenarios, where patch diversity is also of importance. Multi-objective exploration might be beneficial for several reasons, all depending on the attributes of the patches (or resources). For example, the patches can differ in quality, hence constraining the search to a small subset of the number of patches might not optimize the total quality gain. Patches might also contain different types of resources, e.g. water and food, which are both necessarily for survival of the forager. Hence, following Wosniack *et al.* [14], we define the *patch search efficiency* as

$$\eta_p = \frac{1}{d} \frac{N_p^*}{N_p} \sum_{m=1}^{N_p^*} n_m \left(1 + \frac{|\bar{n} - n_m|}{n_m} \right)^{-1}, \quad (2.16)$$

where d is again the total distance traveled by the forager, n_m is the number of resources in patch m , $\bar{n} = M^{-1} \sum_m n_m$ the mean number of found resources per patch and N_p^* the number of distinct patches visited. Note that the denominator is minimized if $\bar{n} = n_m$, meaning that to optimize η_p , all patches should be visited an equal number of times. Mathematically, the search efficiency of Eq. (3.5) is recovered if $N_p^* = N_p$ and $\bar{n} = n_m$. This represents a homogeneous environment, i.e. each ‘patch’ only contains a single resource. Furthermore note that one can adapt the definition of Eq. (2.16) to account for the interpatch differences, by labeling resources by their different attributes (see [14]). Extending both the memory model and the search efficiency to account for different types of resources is considered a topic for future work.

2.4 Results

2.4.1 Random search without memory ($\beta = 0$)

Let us first discuss the random search that occurs when the truncation probability equals 0, which corresponds to $\beta = 0$. In this case, there are

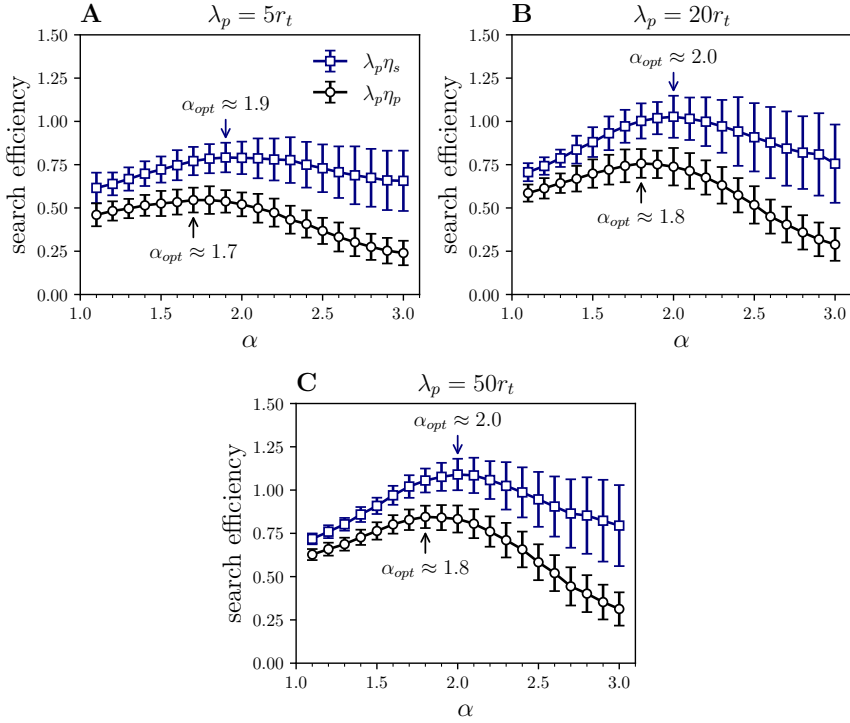


Figure 2.3: Normalized (patch) search efficiency for $\beta = 0$, i.e. random Lévy search without memory, for different Lévy walk parameters α and different intrapatch mean free paths λ_p . Blue squares represent the search efficiency $\eta_s \lambda_p$ (Eq. (3.5)), while black circles indicate the patch search efficiency $\eta_p \lambda_p$ (Eq. (2.16)). Optimal Lévy parameters α_{opt} are indicated with arrows. The search efficiency is always optimized for values $\alpha_{opt} \approx 2$, while the patch search efficiency is optimized for slightly lower values of α . Error bars represent one standard deviation.

no bouts of informed movement; the entire search is a random search. We study the random search efficiency in heterogeneous environments as a comparison against the proposed memory models. We measure the (patch) search efficiency of the foraging process for different values of the intrapatch mean free path λ_p . Results are shown in Fig. 2.3, and identify the existence of an optimal Lévy parameter α_{opt} . The search efficiency η_s is maximized for $\alpha_{opt} \approx 2$, regardless of the value of λ_p , congruent with existing work that discusses the robustness of optimality of the Lévy walk in heterogeneous environments (see e.g., [23]).

Recall that η_s is optimized through maximizing the number of resources detected while simultaneously minimizing the traveled distance. Intuitively, this is achieved by interchanging local search within dense

patches (Brownian motion, $\alpha \rightarrow 3$) with global displacements in search of other regions with high resource density (ballistic motion, $\alpha \rightarrow 1$). Sparse patches henceforth lead to intermediate values of $\alpha \approx 2$ being optimal. This is congruent with the well-established optimum in sparse, homogeneous environments [4, 5, 23].

In contrast, the patch search efficiency η_p is optimized by slightly more ballistic strategies, as indicated by the arrows that highlight the optimal value for α (see Fig. 2.3). Recall that η_p is optimized when each patch is visited an equal number of times. Hence, due to the truncation of the walk at resource detection, it is more difficult to exit a patch when patches are dense (small λ_p), while the forager needs to exit its current patch in order to maximize the patch search efficiency. The shift of the optimum to (slightly) more ballistic strategies is therefore resulting from the fact that these foragers are more likely to exit the patch and thus are more likely to increase the number of distinct patches visited. As a result, when patch diversity is of key importance, more ballistic strategies are preferred (see also [14] and references therein).

2.4.2 Informed search with memory ($\beta > 0$)

Next, we study the influence of the truncation parameter β on both search efficiencies. Note that the informed search is executed only after the model has been initialized, which occurs after the minimum number of resources $N_{\min} = 100$ have been detected through means of a random search. In other words, the informed search is always preceded by a random search, until a minimal number of resources have been detected through means of a random search. The resources found in this initial random search, act as the prior data for initializing the ensemble of GMMs that are incrementally updated with new batches of resource positions found during the informed search. In all following experiments, we set the number of ensemble members $K = 3$, and the minimum and maximum number of components per member to be $1 \leq M_k \leq 10$. Note that the maximum number of components is equals to the number of patches N_p . For the Lévy parameter α , we chose the optimal value conform the random search, $\alpha_s = 2$ for the search efficiency η_s and $\alpha_p = 1.8$ for the patch search efficiency η_p . Results for various intrapatch mean free paths are shown in Fig. 2.4, which obviously indicate optima with respect to the memory strength β .

First, the search efficiency is maximized when memory effects are strong, Fig. 2.4A-D. As indicated earlier, revisitation of a select number of resources is highly beneficial for optimizing the search efficiency as defined in Eq. (3.5). Indeed, as illustrated in Fig. 2.5, the total number of unique resources (and patches) visited decreases when the memory strength increases. Hence, the forager indeed favors revisitation of a small fraction of the total number of resources, since its explorative motion is truncated due to strong memory effects, resulting in more informed move-

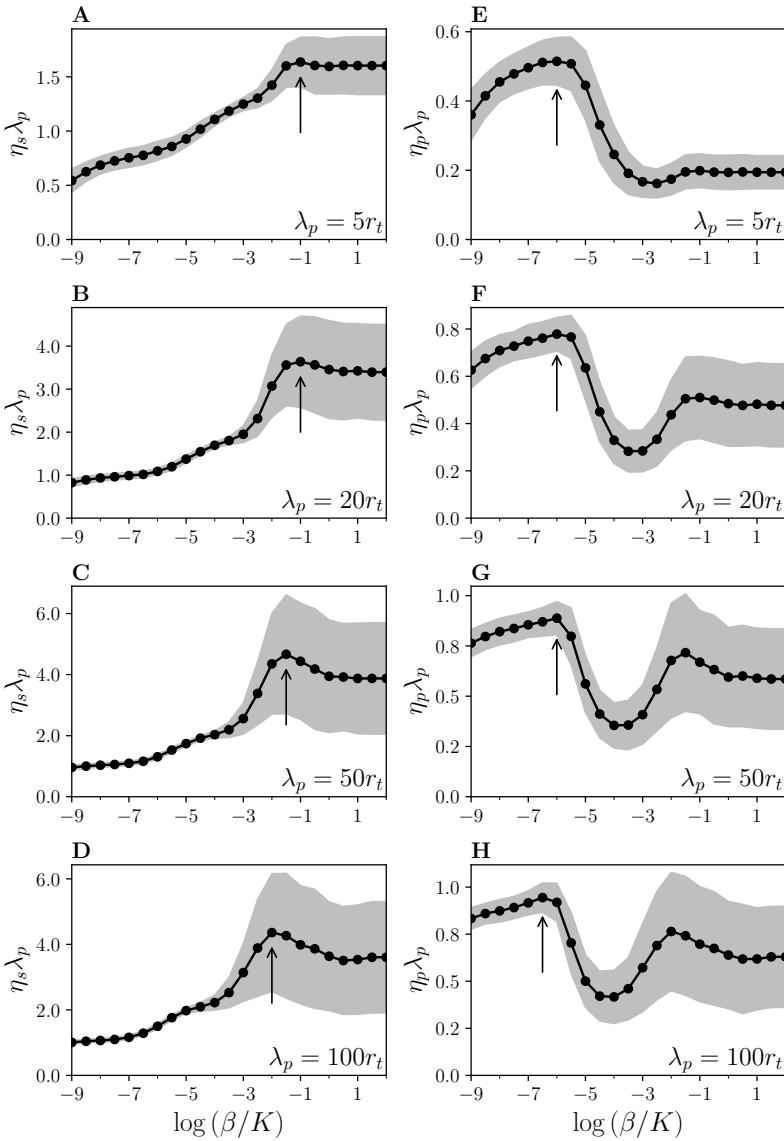


Figure 2.4: Normalized search efficiency $\eta_s \lambda_p$ and patch search efficiency $\eta_p \lambda_p$ versus the scaled memory strength β/K for several intrapatch resource densities λ_p . Low values of β/K correspond to highly explorative foragers, while larger values correspond to foragers that adopt their model quickly. For the left column $\alpha = 2.0$ and for the right column $\alpha = 1.8$. Arrows indicate maxima, shaded areas represent one standard deviation.

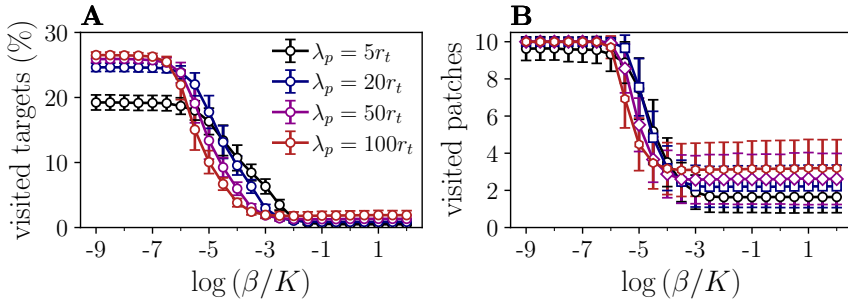


Figure 2.5: Unique resource and patch encounters versus the scaled memory strength β/K . Error bars represent one standard deviation. (A) The percentage of unique resources visited, for several intrapatch mean free paths λ_p . The decrease indicates that, as the memory strength increases, the forager favors revisitation of a select number of resources over more explorative behavior that displays a wider variety of unique resources detected. (B) The number of unique patches visited displays similar characteristics, furthermore indicating that foragers prefer to not venture out into interpatch space, as to maximize the resource encounter rate within a few patches found during the initial exploration (see also Fig. 2.2).

ment towards the detected clusters of resources. Furthermore note that the search efficiency decreases when memory effects strengthen. Since searches are ended after a fixed number of resources have been detected, the increase in variance results from an increase in variance of the distance traveled, as is shown in the inset of Fig. 2.6. Note that the variance increase is more substantial in very sparse environments, since resource detection is inherently more difficult in those cases. Due to this sparsity, goals sampled from the spatial distribution learned over the resources detected during the initial random search may not be in close proximity of an actual resource. Hence, the informed movement potentially has to be repeated several times, which results in the observed variance increase in the travel distance and subsequently both search efficiencies. Furthermore note that, as expected, more distance needs to be traversed to complete the search task whenever the resource sparsity increases.

Next, the patch search efficiency displays interesting trends. It is optimized for much more explorative strategies, with β as low as 10^{-7} (conform to the explorative forager in Fig. 2.2). Thus, increased memory strength actually decreases the diversity of patch visitations, as also discussed above (see Fig. 2.5), and more explorative behavior is preferred. This originates from the choice of incremental learning of the ensemble of GMMs, since the ensemble members that were learned from the initial batch of detected resources can be sampled from much further into the informed search process. The influence of the initial set of detected resources can be adapted by the aforementioned forgetting rate, which controls how

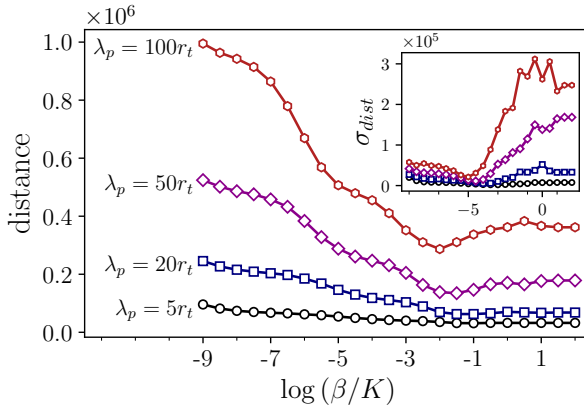


Figure 2.6: Distance traveled versus the scaled memory strength β/K . Inset shows its standard deviation. More sparse distributions require longer distances to be traveled by the forager and additionally increase the variance due to the fact that rates of detecting resources in very sparse environments are determined by chance (see text).

conservative the forager is when new resources are encountered. However, even when the forgetting rate is tuned such that all old resource locations are forgotten, i.e. the incremental updating of the GMM is effectively replaced by learning a new GMM over the new resource locations, the new resource locations will most likely be around the old resource locations when memory effects are strong. Hence, most of the different patches visited during the task are already visited during the initial random search, and memory does not increase the chance of detecting faraway regions rich in resources. In other words, foragers that strongly depend on their memory, are much more conservative and seldomly venture outwards to discover new patches, which detracts the patch search efficiency. If a high diversity of patches is preferred (or required, see Section 2.3.2), high memory strengths are suboptimal. This indicates the long-term memory effects are not beneficial towards optimizing resource diversity.

The patch search efficiency displays a minimum for intermediate memory strengths, which is more pronounced when resources are sparsely distributed within the patches, see Fig. 2.4E-H. These minima arise from long bouts of exploration wherein no resource was detected, only truncating the walk in favour of informed motion after a relatively large number of steps. These bouts result in the forager venturing out into unknown territories. However, due to the sparsity of the resource distribution, it is unlikely to detect resources during these ventures. Hence, the forager travels more (unnecessary) distance before giving up on the search and traveling back to known territories. Such hesitations, i.e. no true commitment to explo-

ration, result in an increase in the travel distance that is not accompanied by an increase in the number of resources detected (as indicated in Fig. 2.5), hence the resulting decrease of the patch search efficiency for intermediate values of β .

Finally, the patch search efficiency again increases when the memory strength increases, compared to intermediate memory strengths. This increase originates from the efficiency of the revisitation strategy of the forager, as the number of unique resources (and patches) visited do not change when the memory strength increases further (see Fig. 2.5). However, venturing into unknown regions is suppressed due to higher truncation probabilities resulting from larger values of β . Essentially, this results in similar revisitation as intermediate memory strengths exhibited, while decreasing the distance traveled in between resource revisitations (see Fig. 2.6). In turn, this reduction in travel distance increases the patch search efficiency, however the increase does not rise above the optimum reached for more explorative strategies, realized through smaller values of β .

2.4.3 How does memory affect walk characteristics?

Next, we discuss the characteristics of the walk that results from both the truncation at resource detection as well as the memory. As illustrated in the example trajectories of Fig. 2.2, memory greatly influences the walk characteristics. Specifically, the distribution over walk distances changes from a power law to an exponential distribution, which does not possess the fat tails characteristic to power law distributions. Stronger memory effects (i.e. greedy foragers, high β), tend to more localized behavior around the first few patches wherein resources are detected, hence disposing of the statistically relevant long-range displacements typical of the Lévy walk. Moreover, the power law tail observed in Lévy walks is often absent when resource densities are high, regardless of memory [2].

We demonstrate this in more detail by executing an informed search for fixed number of resources, wherein we define an *episode* to be a time window wherein the model remains fixed. Thus, an episode ends at the same time the random search is truncated and the model is (incrementally) updated. First, the model disagreement φ is plotted, including the single step truncation probability $p(1, \varphi)$, in Fig. 2.7A,B. The model disagreement decreases as the number of episodes (model updates) increases. Naturally, the corresponding truncation probability depends heavily on β , as the intermediate forager has a single step truncation probability of effectively 0 (see Fig. 2.7A). However, the greedy forager is very likely to truncate its random search after a single step after a few model updates due to the combination of a low model disagreement φ and high value of β . As a result, the greedy forager repetitively only visits resources from memory and omits exploration entirely.

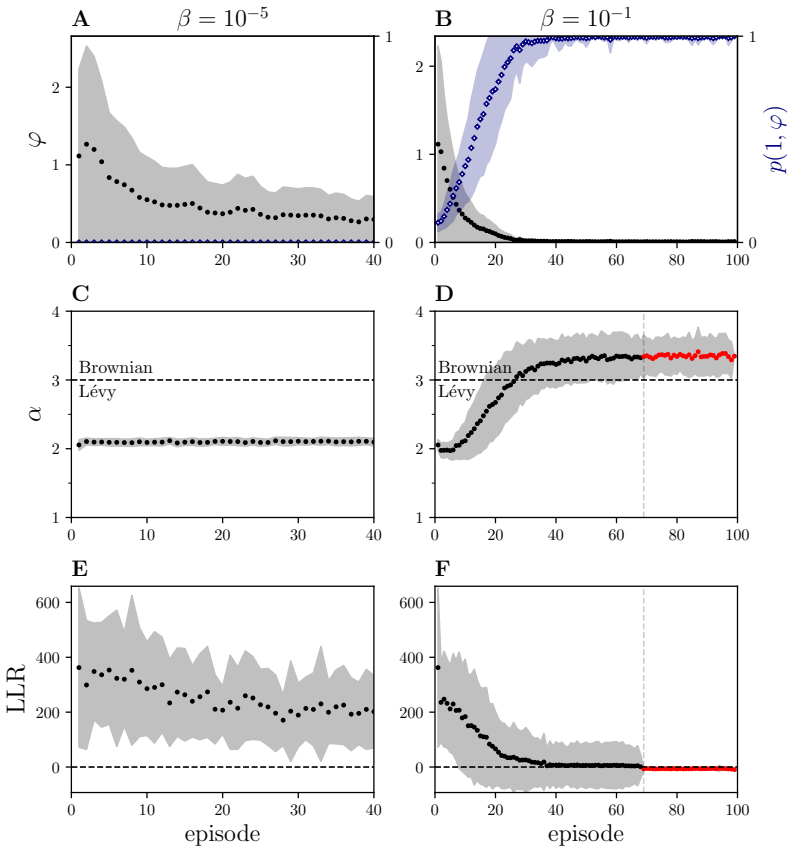


Figure 2.7: Influence of memory on the power law distribution over walk distances for foragers searching with Lévy parameter $\alpha = 2$ in an environment with $\lambda_p = 20r_t$. Two types of foragers – intermediate ($\beta = 10^{-5}$, left), and greedy ($\beta = 10^{-1}$, right) – have executed an informed search to search for 10^4 resources. (A,B) The average model disagreement φ continuously decreases as the model is updated. The truncation probability $p(1, \varphi)$ is shown in blue, with $L_0 = 1$. (C,D) The approximate power law exponent computed from the distribution over walk distances, and (E,F) the corresponding log-likelihood ratio between a power law distribution and an exponential distribution. Red colors indicate episodes for which the average $LLR < 0$, while the vertical dotted lines highlight the episode for which this first occurs. Note that the intermediate forager displays a power law distribution across the full task, while the greedy forager changes its walk distance distribution to an exponential (Brownian) one as its model is incrementally updated. Each point shown corresponds to a single episode (see text). Shaded areas represent one standard deviation, averaged over 50 different realizations.

Next, we record the walk distances within each episode, which can be truncated due to resource encounters. Using the distribution over walk distances within each episode, we can fit a (truncated) power law distribution and compute an approximate value for the Lévy parameter α . However, fitting a distribution is misleading due to the fact that the underlying data might not be described by the candidate function [57–60]. Therefore, the log-likelihood ratio (*LLR*) between a (truncated) power law, which indicates anomalous diffusion, and an exponential distribution, which is indicative of Brownian-like diffusion, is computed. For this computation, we use existing and well-established libraries [58].

We report results for two distinct types of foragers; intermediate and greedy (see Fig. 2.2). The naive forager is not shown, since those do not adapt their model due to their truncation probability being effectively zero, hence the search consists of a single episode which obeys a power law distribution over walk distances (results not shown). As seen in Fig. 2.7, the intermediate forager has walk distance distributions that obey a power law, up until the task is completed. In contrast, the greedy forager changes its walk behavior to Brownian motion the more its spatial distribution is updated. The result is that, approximately, both the fitted power law component $\alpha \geq 3$, and *LLR* < 0 , indicating that the distribution over walk distances does not follow a power law but is more likely to obey an exponential distribution, i.e. Brownian motion [2]. Memory thus affects the walk distance distribution, inducing less diffusive motion in favour of revisitation of a select area rich in resources. This decrease in diffusivity directly results in the previously mentioned suboptimal patch search efficiencies reached when memory effects are strong, since those are optimized with more ballistic strategies (see Fig. 2.3 and [14]).

Whereas assigning power law distributions to empirical datasets of walk distances needs to be handled with caution [59, 60], our rudimentary study of the underlying distributions illustrates that the diffusivity is not necessarily determined by the underlying sampling procedure [2]. Indeed, random walks with memory induced relocations to previously visited locations, have been shown to display subdiffusion [31]. Moreover, Brownian motion induced by memory is favored over more ballistic Lévy walks when resources are more difficult to encounter [11], indicating that the switch to more Brownian-like motion aids non-destructive resource detection in very sparse environments. Additional careful analysis on the effect of spatial memory on the movement pattern of the forager is beyond the scope of this paper.

2.5 Discussion

We have investigated the effects of spatial memory on the search efficiency in patchy environments. Spatial memory constituted of an ensemble of Gaussian mixture models. The resulting hybrid foraging strategy, alter-

nates Lévy walks as random searches with memory induced walks. The truncation probability, which indicates the switch between the two distinct walks, increases with the number of steps since the last resource detection and decreases of the model disagreement. We have shown that non-destructive foraging is optimized when memory effects are strong and the search efficiency is defined solely through the rate of resource detection per unit traveled. However, strong memory effects result in high revisitation rates of a select few resources, often within a small fraction of the available patches. Thus, explorative behavior is penalized due to increases in the traveled distance not being accompanied by similar increases in the number of resources detected. This identifies a trade-off between the search efficiency and patch diversity. The trade-off is not trivially solved by intermediate memory strengths, since we observed the patch search efficiency to be minimized when memory strengths are intermediate. As a result, the benefits of memory heavily depends on the needs of the forager. If a high diversity of resources is required for survival, then more explorative motion is preferred, whereas memory serves more useful in sparse environments in which resources can be revisited indefinitely.

Where we have assumed an infinite regeneration rate by assuming non-destructive foraging, we believe that the results might also be beneficial for finite regeneration rates. Notably, the benefits the forager obtains from using a spatial memory strongly depend on the regeneration rates of resources. When resources are sparsely distributed, but do regenerate over potentially long periods of time, memory might serve as a very useful tool that increases survival chance due to enabling revisitation of previously exhausted patches that have regenerated [61]. Moreover, finely tuning memory strengths with potential periodicity of the availability of the resources, e.g. seasonal growth, might greatly reduce search times and energy consumption and as a result increase the search efficiency [62]. In addition, random walks without memory also exhibit a switch from superdiffusive walks to ballistic motion as the resource regeneration time changes from zero (non-destructive) to infinity (destructive) [50].

Further, using an ensemble of GMMs as a spatial distribution enables researching attribute dependent behavior. Since each member of the ensemble consists of a mixture of Gaussians, weighting the Gaussians differently when sampling goal states can be coupled to certain attributes of the resources whereover the Gaussian was fitted, e.g. patch quality. Additionally, each member can represent different types of resources in order to account for balanced resource detections, furthermore accompanied by the aforementioned possible adaptations of the patch search efficiency. Future studies might indicate that foragers that aim to optimize overall resource diversity, benefit more from an ensemble of differently weighted spatial distributions.

Lastly, it is important to note that the *Lévy walk paradigm* [63], i.e. that forager movement follows a Lévy walk, has been criticized as being unre-

alistic [46], mainly because traditional implementations of the Lévy walk omit directionality resulting from a continuous decision-process. An effect of the continuity of the foraging process, is that any organism can change its behavior at any instant in time [64]. In this work, the decision process of the forager is continuous as the forager decides to continue or truncate the search based on its current available information from both from its perception as well as its memory. An additional critique was that the spatial scales whereover the walk characteristics are determined should be relevant to the foraging process, something that we have achieved by sampling walk distances using a truncated power law. Hence, while further investigation on the motion of foragers is warranted, we have directly tackled the main criticisms of the Lévy walk paradigm by inclusion of the truncation probability depending on memory.

This work presented in this chapter indicates that spatial memory is not necessarily beneficial towards detecting a diverse set of resources. We have identified strengths and weaknesses of a potential spatial memory candidate, which suggests that the balance between using memory versus naive random walks is fickle and is in much need of further study.

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3

Group size and resource fractility drive multimodal search strategies: a quantitative analysis on group foraging

Abstract

In the previous chapter, resource distributions were effectively static as foraging was considered to be non-destructive. Instead, this chapter will focus on destructive foraging. Learning a spatial distribution over a dynamic resource distribution is, however, most often likely ineffective, and hence we omit learning spatial memory entirely. As the problem of optimizing individual random searches in such environments has been studied extensively, we additionally shift our focus to studying foraging behavior in a group of competitive foragers. We introduce an agent-based model wherein competition arises from foragers having to compete for a limited set of resources. We consider foragers that change the characteristics of their random search upon entering a patch, by switching from an extensive search with long-range relocations, to intensive, more localized searches. We study a system where foragers can monitor the search behavior of nearby conspecifics and become attracted to those that are searching intensively, as this behavior signifies a patch rich in resources. By controlling resource patchiness, we quantitatively determine advantages of group foraging on individual foraging efficiencies. Our results indicate that, when resources are sufficiently clustered, joining nearby others in their successful foraging efforts is shown to become an efficient strategy. However, when group sizes increase, joining others is disadvantageous due to increased levels of competition on the patches. We further examine individual advantages by measuring the variation in resource intake rates. Interestingly, our results show that individual advantages are highest in conditions wherein group advan-

tages are lowest. This indicates that, while foraging in groups can be advantageous for the individual under certain environmental conditions, foragers often resort to so-called 'low mean, low variance' strategies instead. The results presented in this chapter supports the notion that foraging in groups does not necessarily result in increased foraging efficiencies, but that it might facilitate more strict incentives such as survival.

3.1 Introduction

Foraging is critical to the survival of many animal species. To this end, many animals exhibit optimized foraging behavior. Often, precise resource locations are unknown, making optimizing random searches for individuals of vital importance [2–4]. In addition, foragers within a group might benefit from interactions with others in order to further increase their foraging efficiency [5, 6]. For example, detecting successful nearby conspecifics and joining them has been a well-documented phenomenon in natural systems [7–12]. However, when group sizes increase, intraspecific competition additionally increases [13–20], in turn leading to possible overpopulation or overconsumption of areas rich in resources. Ultimately, this can reduce the average resource consumption rate of individuals. This indicates that foraging efficiency is not only highly dependent on the resource distribution, but also on individual decision processes and interactions between foragers [21].

Traditionally, foragers joining successful others have been studied in the context of information sharing systems [22, 23] or producer-scrounger systems [24, 25]. In information sharing systems, foragers individually search for resources while simultaneously monitoring the behavior of nearby conspecifics, thus allowing unsuccessful foragers to join successful others [26]. Such joining mechanisms can reduce variations in resource intakes as it equalizes the distribution of resources, possibly leading to higher group search efficiencies [12, 27]. In the producer-scrounger framework [23, 28], individuals are typically considered to be either a scrounger or a producer. They can choose to search independently for resources (producers), or take advantage of others (scroungers), for example by joining a patch and competing for resources. Thus, the effectiveness of scrounging depends heavily on the number of scroungers relative to producers. Producer-scrounger models have been used to model group foraging [25, 29], where field studies have identified intricate producer-scrounger dynamics within populations of baboons [30], rooks [31] and finches [32], among others. While these dynamics critically depend on the environment, very little is known about the precise influence of resource distributions and availability on the effectiveness of group foraging.

In general, advantages of joining others increase as resources become more difficult to locate. When resources are readily available, an individual does not need to be joining others, as individual resource encounter

rates are high. In contrast, many natural landscapes have resources distributed in patches, leading to fragmented distributions [33, 34]. Most often, separate patches are the result of power laws that describe the underlying resource distributions [35, 36], leading to scale-free, fractal resource landscapes [37–45]. Such resource distributions typically increase the benefits of joining, since resources themselves are more difficult to locate, but patches contain many resources [46]. However, it is important to consider that intraspecific competition – as foragers are competing for the same set of (limited) resources – highly influences the advantages of joining strategies. Quantitative results on critical degrees of fragmentation or clustering, and levels of competition (group sizes and joining ranges), are to the best of our knowledge absent from current literature.

Besides joining nearby successful conspecifics, individual search strategies are still of critical importance. Data logging techniques have resulted in attributing existence of heavy-tails in the distribution of flight lengths used in random searches [43, 47], thus allowing for the description of random searches as Lévy walks or flights [3, 48]. Whereas the robustness of these Lévy searches has been widely established [2, 4, 49–51], whether animals truly execute Lévy walks is currently still up for debate [52–57]. Nevertheless, increasing evidence shows existence of Lévy walk characteristics across a wide variety of organisms, ranging from micro-organisms such as bacteria [58], cancer cells [59] and T cells [60] to aquatic animals [61], and from insects such as honey-bees [62] to mammals such as deer [63, 64] and even human hunter-gatherers [65]. Moreover, recent theoretical advances seem to point towards Lévy walks as random searches for optimal area coverage [66] and for optimising the time needed to detect sparse targets of different sizes [67].

The characteristics of Lévy walks depend heavily on environmental influences [61], where individuals generally display lower levels of dispersion when resources are plentiful. To model this, the (non-adaptive) Lévy walk framework originally proposed by Viswanathan et al. [2] can be adapted to a multimodal (adaptive or composite) search [68, 69]. Different levels of diffusion in each mode represent differences between global displacements (exploration) and localized searches (exploitation), where switching between the modes can be mediated by the state of the forager. Both resource availability and resource distribution significantly impact the effectiveness of composite random searches. This raises the question if there exist optimal search strategies that take into account resource distribution and (local) conspecific densities. Most likely, searches that optimize foraging efficiencies balance individual searches with group behavior such as aggregation [6, 70].

This work aims to provide a quantitative analysis on the effects of intraspecific competition on the individual- and group-level foraging efficiencies in fractal resource landscapes. It acts as a first effort to systematically investigate observed behavioral traits in foragers, and how these

depend on the resource landscape and interactions between individuals. To this end, we study multimodal random searches in the information-sharing framework. More specifically, we study the intricate interplay between the resource landscape, the individual decision process, and the benefits of joining successful conspecifics. We employ an agent-based model that implements a group of foragers that compete for resources available within the environment. Competition arises from the fact that foraging is destructive, i.e. resources disappear after consuming them, leading to areas initially rich in resources becoming depleted over time.

Within our model, we first introduce a bimodal (adaptive) Lévy search consisting of an extensive and an intensive search mode. The extensive search is defined by choosing parameters of the Lévy search such that random searches become highly diffusive, representing exploration. In contrast, assuming resources are sufficiently clustered, the forager switches to more localized random searches upon resource detection, representing exploitation. Using this model, we show that when intensive searches are of relatively long duration, i.e. sufficient exploitation, ballistic extensive searches are always the most efficient. Interestingly, due to intraspecific competition, individual searches by a single forager are, on average, always more efficient than those achieved by groups of foragers. We find that when resources are not clustered, distributions over resource intake rates are log-normal, but this feature disappears beyond a certain degree of clustering. The reason is that intraspecific competition results in skewed distributions over resource intakes, meaning that a significant fraction of the group find little to no resources when those are significantly clustered.

Afterwards, we then extend the bimodal model to a trimodal one, wherein foragers can additionally be attracted towards successful nearby conspecifics. Here, successful foragers are those that have recently detected a resource, and are thus executing intensive searches. Therefore, we consider switches to intensive searches to act as a cue to nearby others, effectively identifying the forager as an attractor. By introducing attraction towards successful conspecifics, we show that log-normal distributions are recovered over the full range of resource landscapes that we consider, displaying more equal resource intake with lower variation. Furthermore, we study the foraging efficiency more quantitatively by comparing systems of foragers that join successful others with systems of non-interacting foragers. We find that there exist optimal intermediate joining ranges, which decrease in size as relative resource availability decreases. Thus, we show that joining others results in higher average foraging efficiencies only if (i) resources are clustered to some sufficient degree, and (ii) group sizes do not become too large. More interestingly, we find that in resource landscapes where joining does not increase individual resource intake rates, the variation in resource intake decreases. This highlights that many natural systems might not execute optimal foraging *per se*, but instead favour strategies that result in small variation, as long as minimum energetic con-

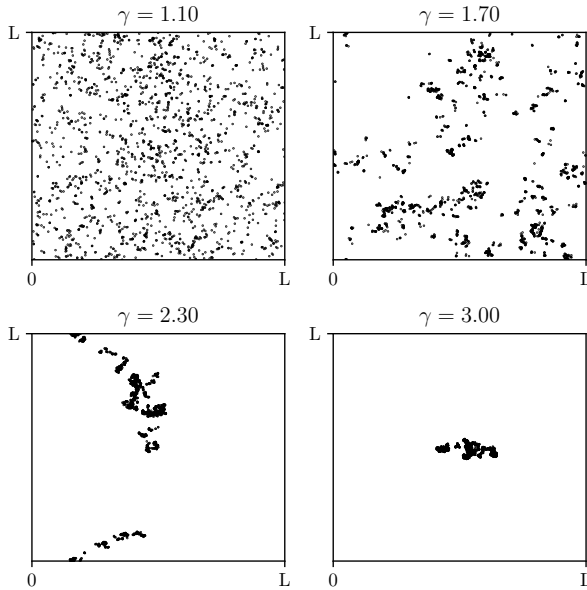


Figure 3.1: Examples of typical resource distributions of $M = 2048$ resources in the $L \times L$ environment for different Lévy parameters γ . The periodic boundary effects are apparent when γ decreases, resulting in increasingly uniform distributions for $\gamma \rightarrow 1$. In contrast, high values of γ result in highly clustered resource distributions. Resource landscapes with intermediate values of γ contain multiple clusters separated by large empty spaces.

straints are met.

We have organized this chapter as follows. First, we introduce the fractal resource landscape in Section 3.2.1, and discuss the bimodal and trimodal Lévy searches in Section 3.2.2, and Section 3.2.3 respectively. In Section 3.3 we present our numerical studies of agent-based model on the foraging task, and discuss the relevance to existing literature. Finally, we conclude our work in Section 3.4 and present an outlook on the implications of our work.

3.2 Model description

3.2.1 The resource landscape

We consider a square, two-dimensional (2D) $L \times L$ environment with periodic boundaries. The characteristics of the resource landscape determine the efficiency of the search strategy used by the foragers. For example, when resources are highly clustered, aggregation might be an efficient strategy, even though levels of resource competition increase [6, 71]. Char-

acterizing the resource distribution is thus of vital importance towards understanding the motivations of aggregations in large-scale systems.

Since we study destructive foraging in fractal resource landscapes, resource dynamics are modeled as disappearance (consumption) of a resource upon detection, and reappearance (regeneration) at a distance sampled according to a Lévy flight. Simultaneous consumption and regeneration ensures that the resource density within the environment stays constant. This is desired as it enables us to study foraging behavior in absence of more invasive effects such as drastic changes in resource availability. Time dependent resource densities that result from external causes, e.g. deforestation, are considered important topics for future research.

We let distances between resources be sampled from a truncated inverse power law, where upper and lower truncation ensure that distributions occur on the appropriate scale [50, 56]. The distribution with Lévy parameter γ is defined as

$$p_\gamma(\ell) = \begin{cases} Z_\gamma \ell^{-\gamma} & \ell_0 < \ell \leq L \\ 0 & \text{otherwise,} \end{cases} \quad (3.1)$$

where Z_γ is the normalization constant and ℓ_0 and L are the minimum respectively the maximum distances. The orientation angle θ between subsequent resource placements is sampled uniformly between 0 and 2π . As such, the generated resource distribution represents a Lévy dust [72, 73], where each point in the flight represents a resource location.

Lévy flights capture different resource distributions, related to the properties of the distribution (see Fig. 3.1). For $\gamma \rightarrow 1$, distances between subsequent resources are large, resulting in a (near) uniform distribution due to the periodic boundaries (see also [66]). When $\gamma \geq 3$, the resulting pattern is highly clustered, often resulting in resources being contained in a single, dense cluster. Intermediate values $1 < \gamma < 3$ result in clumped distributions, where multiple aggregates are separated by large empty spaces. In principle, when the number of resources $M \rightarrow \infty$, due to the periodic boundary conditions all values of γ will asymptotically converge to the same distribution, being dense and uniform [50]. However, since realistic environments have a finite number of resources, the significant structural differences for different values of γ become apparent even for relatively large values of M , as seen in Fig. 3.1.

3.2.2 Individual behavior

Within the clustered resource landscape, we consider a system of N foragers initially distributed uniformly within the environment. In our experiments, resources can be detected by the foragers within a detection radius R . Each individual forager randomly searches the environment for resources by executing a (bimodal) adaptive Lévy walk with parameter α

[69, 74]. It is important to note here the difference between a Lévy flight and a Lévy walk, with only the latter having a finite velocity that implies a spatiotemporal coupling [48, 50]. Then, similar to Eq. (3.6), flight lengths are sampled from an inverse power law as

$$p_\alpha(\ell) = \begin{cases} Z_\alpha \ell^{-\alpha}, & \ell_0 < \ell \leq L \\ 0 & \text{otherwise} \end{cases}, \quad (3.2)$$

where Z_α the normalization constant. Foragers walk along the sampled flight lengths with step size (fixed velocity) ℓ_0 , with the direction ϕ sampled uniformly from 0 to 2π . The parameter α defines the spatial characteristics of the movement. Lévy walks encompass a wide range of different movement patterns (diffusion), ranging from ballistic motion for $\alpha \rightarrow 1$ to anomalous diffusion for $1 < \alpha < 3$, and normal diffusion (Brownian motion) for $\alpha \geq 3$. It is critical to note that convergence of Eq. (3.2) towards a Gaussian process is ultraslow [75], hence the general characteristics, e.g. the heavy tail, of the Lévy distribution are conserved during our finite time foraging task. For a more detailed discussion on Lévy flights and Lévy walks, and their implications for foraging, we refer the interested reader to more in-depth studies [3, 48].

In this work, we let the actual value of α depend on the mode the forager is in. The bimodal search consists of an extensive search mode with parameter α and an intensive search with parameter α' . Initially, each forager starts in the extensive search mode wherein the forager explores the environment using a Lévy walk parameter $\alpha \leq 3$. At resource detection, the forager switches to the intensive mode with $\alpha' = 3$ (Brownian motion), under the assumption that the resource distribution is clustered. Such a composite random walk has been observed in numerous animal species (see e.g., [76–78] and references therein). Effectively, these search strategies allow individuals to focus their efforts on areas rich in resources, while simultaneously minimizing time spent in areas void of resources [3]. While such composite random walks have been found to accommodate higher search efficiencies for single foragers [74, 78], to the best of our knowledge such composite Lévy searches have not been studied extensively in group foraging scenarios (but see [6]).

In our bimodal Lévy search, the intensive search mode can at any point in time be truncated with probability p_β , effectively switching back to the extensive search. Naturally, this truncation strongly influences the efficiency of the search. When exactly a forager truncates its current intensive search should depend heavily on the resource landscape. Similar to previous studies [79, 80] (as discussed in Chapter 2), it is therefore sensible to have the truncation probability depend on the recent success of the forager. In general, when the forager assumes a clustered resource distribution, intensive searches should be longer, while short intensive searches should be preferred when resources are more spread out. To this end, we define

the *switching probability* for switching back to the extensive search from an intensive search by

$$p_{\beta}(d_0) = 1 - \exp\left[-\frac{\beta d_0}{\ell_0}\right], \quad (3.3)$$

where β is the *switching parameter*, and d_0 the distance traveled without resource encounter. Thus, the forager is more likely to exit its current intensive search if it has not detected a resource in some time; a decision that is influenced by the switching parameter β .

Essentially, the switching parameter β determines to what extent a forager should ‘exploit’ the current region, assumed by the forager to be rich in resources (see also [69, 78]). Lower values of β indicate long intensive searches, while higher values of β result in short intensive searches. Note that setting $\beta = \infty$ recovers the unimodal Lévy search, where there does not exist an intensive search and the forager simply searches the environment while maintaining $\alpha \leq 3$ (see Appendix 3.A). Further note that a switch to an intensive search at resource encounter is only beneficial when resources are clustered. Thus we implicitly make the assumption that foragers expect the resource landscape to be clustered to some degree. If this assumption is false, composite random walks do not necessarily optimize random searches [69].

3.2.3 Attraction to conspecifics

Next we describe attraction towards nearby conspecifics that are within a perception range r . In general, conspecific perception ranges are larger than resource perception [70, 81–85], i.e. $r \gg R$. We model attraction towards recently successful nearby conspecifics through aborting the current search direction in favor of travel towards the closest attractor. Here, recently successful foragers are those who are executing intensive searches, i.e. foragers are attracted to those who have recently detected resources and are thus likely to be within a patch. This type of attraction has been observed in many natural systems, such as, but not limited to, worms [11], fish [12], bats [20, 46], seabirds [14, 82, 86, 87] and gazelles [70]. It relies on use of *public information* [83, 88, 89], where the information that is considered public in this work is the location and the search mode of nearby conspecifics.

Attraction is modeled through sampling a travel angle from a wrapped Cauchy distribution (WCD), making attraction to be modeled according to a correlated Lévy random walk with parameter α [90]. Note here that attraction considers the same Lévy parameter α as exploration. The mean of the WCD is the angle between the focal forager and the nearest successful conspecific (the attractor). The shape parameter ρ of the WCD depends on the distance towards the nearest attractor d_{near} (see Fig. 3.2). More specifi-

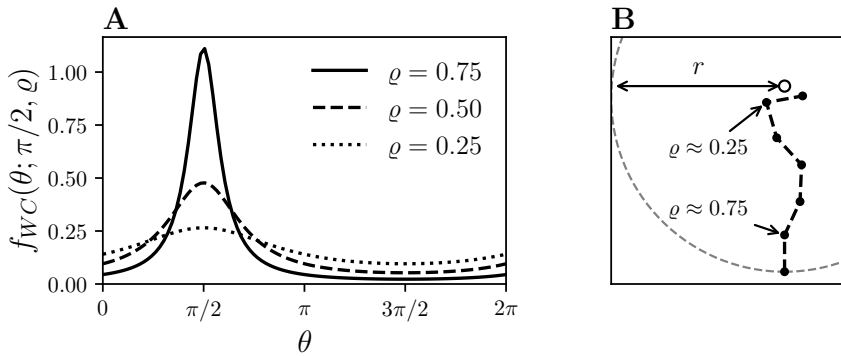


Figure 3.2: (A) Wrapped Cauchy distribution f_{WC} for different shape parameters ρ with center angle $\pi/2$. (B) Simplified typical attraction pattern for a focal forager (\bullet) getting attracted to a successful forager (\circ) within the attraction radius r , with initial angle of attraction $\theta = \pi/2$. Travel direction is sampled according to the wrapped Cauchy distribution with $\rho = (d/r)^{1/2}$, where d the distance between the foragers. Typical values of ρ are indicated. Note that as the attracted forager gets closer, the more uniform the sampling of the travel angle becomes.

cally, we define

$$\rho = \left(\frac{d_{near}}{r} \right)^{1/2}. \quad (3.4)$$

The attracted forager executes its Lévy search along this travel direction, meaning that motion is guided towards the nearest conspecific who is currently executing an extensive search. The form of the shape parameter in Eq. (3.4), ensures that the travel angle is sampled more uniformly the closer the attracted forager is to its nearest successful neighbor. Hence, attraction gradually fades the closer the focal forager is to the successful one, in turn executing a localized search when in the vicinity of its nearby successful conspecifics, since travel angles are effectively sampled (near) uniformly as $\rho \rightarrow 0$. Attraction is truncated either when the successful conspecific exits the extensive search (as per Eq. (3.3)), or when the attracted forager detects a resource, after which it switches to an intensive search and becomes an attractor for other nearby conspecifics itself.

Effectively, the type of attraction studied here results in ‘follow-the-leader’-type dynamics, which have been previously discussed, e.g. by Santos et al. [91]. Moreover, such hierarchical structures are indeed very common in natural systems [92–94], and leader-follower relationships have been observed to naturally emerge [95–98]. Within our model, successful foragers in the intensive search mode effectively assume a leader-type role, and foragers attracted to them can be considered as followers. Therefore,

our model of attraction results in ephemeral group formation with temporary leader-follower dynamics. In particular, this contrasts with Santos et al. [91] as they considered permanent groups with fixed leaders. Additionally, our model carries much resemblance with fission-fusion dynamics, where ephemeral groups continuously split and merge, e.g. to exchange information [99–101]. Note that while the specific model of attraction in natural systems might differ, we assume that the above description is a simplification of more complex decisions made at the individual level.

3.3 Results

We employ a Monte Carlo approach by simulating separate foraging tasks in different resource landscapes and initial conditions. The environment size is set sufficiently large at $L = 10^3$, while the number of resources within the environment $M = 2048$ is chosen as to reflect low resource density ($\rho_M = M/L^2 \sim 10^{-3}$, Fig. 3.1). The number of foragers N is a variable considered in ranges typical for (large) foraging systems (typically between 10^2 to 10^3 individuals, see e.g. [6, 70, 102–106]). All results presented below are averages computed over 250 foraging tasks with different initial conditions and random seeds, unless mentioned otherwise. In this work, a foraging task consists of encountering a fixed number of resources within the environment. Here, we consider experiments wherein $2 \cdot 10^4$ resources have to be detected, ending immediately upon reaching that threshold. Note that although this task truncation can influence optimal parameters for the random searches [79], our choice of resource encounters is sufficiently high to alleviate these effects. We have empirically established that increasing the number of to be detected resources does not influence the distributions of, or the numerical values of the to be presented metrics.

3.3.1 A single forager in a fractal landscape ($N = 1$)

To provide insight in the added value of composite random searches, let us first study a single forager ($N = 1$) in a fractal landscape and extract optimal values of α , for different resource distributions defined by γ . Note that optimality here indicates a strategy (i.e., a particular choice of α) that maximizes the search efficiency. In this work, we assume that the cost of foraging for each individual is proportional to the distance traveled (see also [2, 3]). This gives the search efficiency as

$$\eta = \frac{k}{d}, \quad (3.5)$$

where k is the number of resources detected by the forager while traveling a distance of d . Since we truncate the search when a fixed number of resources have been detected, the search efficiency essentially captures how much distance the forager had to traverse during the foraging task.

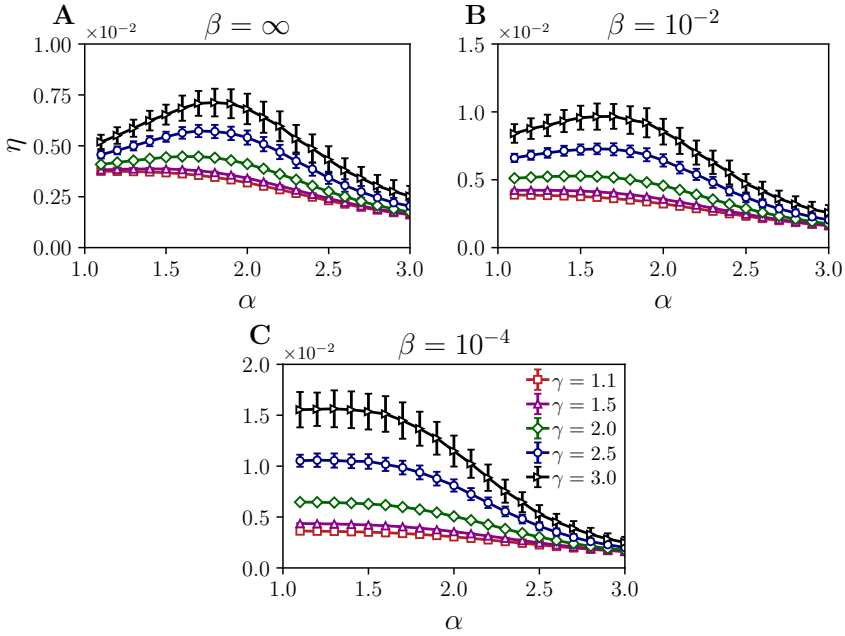


Figure 3.3: Search efficiency η versus α for a single forager ($N = 1$) performing an adaptive Lévy search for different values of β . Resources are placed using a scale-free distribution with Lévy parameter γ . (A) η for the free Lévy walk, i.e. no intensive search (see Appendix 3.A). (B) η for adaptive (bimodal) Lévy searches with (relatively) short intensive searches, and (C) with longer intensive searches. Note the difference of the value of η , where adaptive Lévy walks with finite β have overall higher search efficiencies than when $\beta = \infty$. Error bars represent 1 standard deviation.

Let us set $\beta = \infty$ and thereby recover the unimodal Lévy search that does not adapt its parameter α , as the switching probability $p_\infty = 1$ as per Eq. (3.3) (see also Appendix 3.A). Results are indicated in Fig. 3.3A, and display a cross-over from the widely encountered optimum at $\alpha \approx 2$ as the resource landscape exhibits higher levels of clustering. As γ decreases, the resource distribution becomes less clustered, leading to ballistic searches with $\alpha \rightarrow 1$ to be optimal. These results are in line with existing studies on Lévy searches in fractal resource landscapes, e.g. [50].

In contrast, when the switching parameter β is finite, we observe that more ballistic motion is favored by the forager (Fig. 3.3B,C). Most notably, when the switching parameter β is sufficiently small, i.e. when intensive searches are longer, the optimum shifts to pure ballistic motion $\alpha \rightarrow 1$ regardless of the underlying structure of the resource landscape (Fig. 3.3C). It is critical to note that the value of the search efficiency increases as inten-

sive searches are sufficiently long, especially when the resource landscape is highly clustered. This indicates that the adaptive search with finite β is a more efficient strategy than the unimodal Lévy search with $\beta = \infty$. Obviously, the switching behavior of the forager is only beneficial when resources are sufficiently clustered, leading to foragers assuming *a priori* that resources are clustered to some degree. Therefore, as previously mentioned, in environments where this assumption is false, the search efficiency should decrease. Indeed, resource distributions that are not clustered ($\gamma \rightarrow 1$) display a decrease (albeit minor) in search efficiency as the intensive searches increase in length, since the forager is expecting the resources to be more clustered than they actually are.

This leads us to the following assumption that ballistic extensive searches are always optimal if, (i) the environment is clustered to some significant degree, and (ii) if the forager is changing its search behavior upon resource detection. Thus, the optimal adaptive Lévy search consists of one highly explorative mode (with $\alpha \rightarrow 1$) and a highly exploitative mode (with $\alpha' = 3$). This result has analytically been verified in one-dimensional systems [107], including the fact that such bimodal searches necessarily require some prior information, such as the expected clustering strength of the resources. Our results consolidate this fact in a two-dimensional system.

As a result, in further experiments we consider ballistic extensive searches with $\alpha \rightarrow 1$, as less ballistic searches are less optimal provided the resource landscape is sufficiently clustered. Therefore, β (to some degree) represents the expected local resource density (cluster size) that the forager uses to estimate when it has to leave the patch due to resource exhaustion. This additionally implies that there might exist an optimal value of β , depending on the resource landscape defined by γ , and, as we shall show in Fig. 3.5, these optima are indeed observed in our model. More specifically, optimal values β^* depends on the clustering tendency of the resource distribution, where searches in highly clustered environments are more efficient as the length of intensive searches grows. Most notably, due to intraspecific competition, single foragers benefit more from longer intensive searches than groups of foragers (see also Section 3.3.2).

It is important to note that most animals can estimate local resource distributions to some degree [76, 108, 109], and can often react accordingly, meaning that, in reality, the optimal value β^* is not fixed. In this work, we do not consider more intricate decision processes, but rather focus on the interplay of static search strategies (with fixed parameters) and the resource landscape (with fixed density). Further specifications of the decision process that each individual forager undergoes is considered to be out of the scope of this work.

3.3.2 A non-communicating group of foragers ($r = 0$)

Next, let us consider the bimodal Lévy search in a group of foragers ($N > 1$), wherein no attraction is included, i.e. $r = 0$. Such a system is useful to consider, as it provides a baseline with which to compare when studying the benefits of group behavior. Note that although such a system does not directly imply competition, recall that there exists implicit competition due to the destructive nature of the foragers and forced sharing of the limited set of resources. Resource depletion (over time) reduces the local resource density (not the global density, see Section 3.2.1), hence resulting in foragers individually experiencing environments to be less-clustered than they actually are (see also the discussion on the mean free path in [50]).

3.3.2.1 Search efficiency in group foraging

What effect does the competition for resources have on the search efficiency? To answer this question, we first need to define the group search efficiency η_N . Since we are interested in the efficiency of the group, an intuitive way of defining the group search efficiency is simply the group average of individual search efficiencies

$$\eta_N = \frac{1}{N} \sum_i \frac{k_i}{d_i}, \quad (3.6)$$

where k_i and d_i are the number of detected resources and the distance traveled by forager i ($i = 1, 2, \dots, N$), respectively. Again, the foraging task pertains detection of $K = \sum_i k_i = 2 \cdot 10^4$ resources by the group. The above definition of group search efficiency has been used when studying collective systems [6], however it fails to capture individual differences. Most notably, and as we shall show, resource encounters are not necessarily normally distributed, which makes the mean not reflective of the population. Nonetheless, this metric is informative, provided one accompanies it with detailed descriptions of individual search efficiencies and the variances.

The group search efficiency η_N depends heavily on the individual behavior and interactions between foragers, but additionally depends on the *relative resource density*. This relative measure defines a level of resource availability relative to the number of foragers in the environment. Since in our experiments the number of resources remains fixed, we can change the relative density by changing the group size N . Larger group sizes result in lower resource availability per individual, and thus represent systems with low relative resource density, while small group sizes indicate the contrary.

3.3.2.2 Effects of group size on search efficiencies

When studying the effects of implicit competition, we observe similar effects as when studying single foragers systems, in that the optimal extensive search becomes ballistic as β becomes sufficiently small (Fig. 3.4).

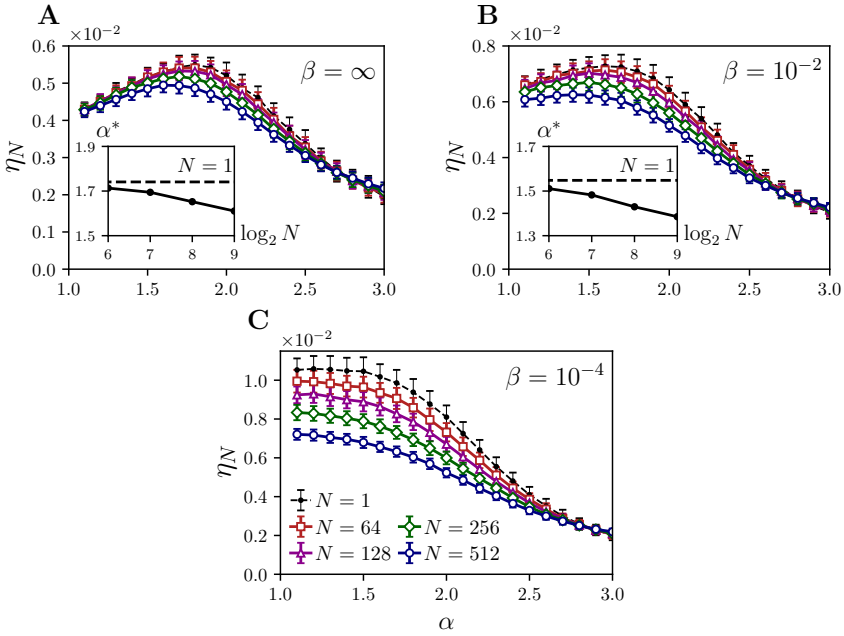


Figure 3.4: Group search efficiency η_N for a non-communicating group of foragers ($r = 0$) versus the Lévy parameter α for several switching parameters β and a fixed clustered resource distribution with $\gamma = 2.5$. Dashed line with black bullets represents the search efficiency η of a single forager within the same resource landscape. Note that $\eta_{N=1} > \eta_{N>1}$ (see text) and that the absolute value of η_N increases as β decreases, indicating that adaptive searches increase the group search efficiency. Insets indicate optimal α^* for the extensive search, where $\alpha^* \rightarrow 1$ as β decreases. Intensive searches were executed with $\alpha' = 3$. Error bars represent 1 standard deviation.

More interestingly, group search efficiencies are lower across the entire range of α compared to a single forager due to competition. Thus, as group sizes increase, group search efficiencies decrease. Additionally, the search efficiencies for unimodal searches ($\beta = \infty$, inset Fig. 3.4A) and bimodal searches with short intensive searches ($\beta = 10^{-2}$, inset Fig. 3.4C) for groups with $N > 1$, display maxima at lower values of α than when $N = 1$. This indeed implies that individuals experience resources to be more sparsely distributed due to others simultaneously foraging destructively [50]. As a result, more diffusive search strategies are, on average, more efficient.

As our results for a single forager ($N = 1$, see Section 3.3.1) indicate that ballistic extensive searches with $\alpha \rightarrow 1$ are optimal, we are interested on the group foraging efficiency for $N > 1$ in this ballistic regime. In Fig. 3.5, we plot the (group) search efficiency for a non-communicating

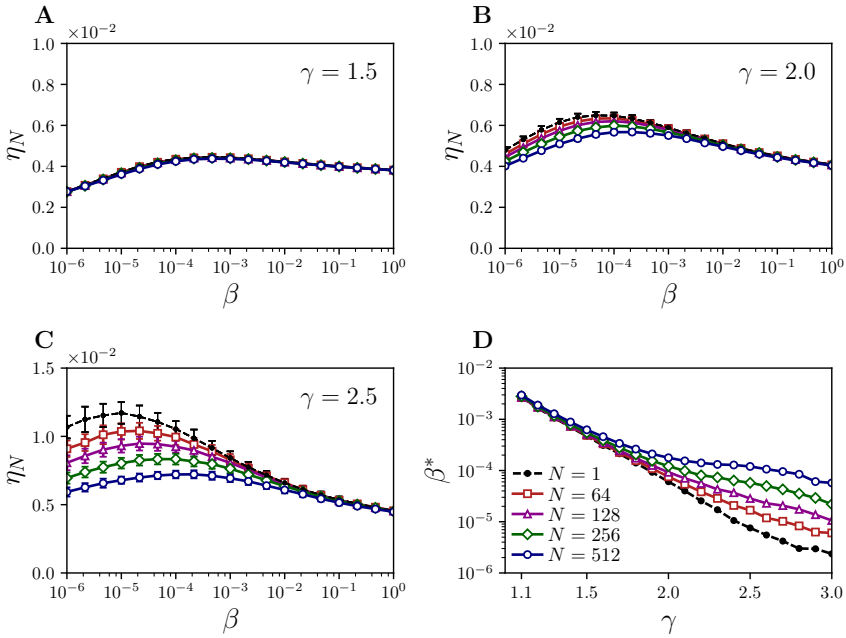


Figure 3.5: Group search efficiency η_N for a non-communicating group of foragers ($r = 0$) versus the switching parameter β , for several group sizes N and different levels of resource clustering γ . Dashed line with black bullets represent a single forager ($N = 1$) within the same resource landscapes. Note that the overall value of the (group) search efficiency notably increases as the landscape becomes more clustered for larger values of γ and that $\eta_{N=1} > \eta_{N>1}$ (see text). Extensive searches were executed with $\alpha = 1.1$ and intensive searches with $\alpha' = 3$. Error bars represent 1 standard deviation. (A) Group search efficiency for low ($\gamma = 1.5$), (B) intermediate ($\gamma = 2$) and (C) strong ($\gamma = 2.5$) degrees of clustering. (D) Value of β that maximizes the (group) search efficiency η_N versus γ , denoted as β^* . Optimal values β^* are computed by fitting each curve in (A)-(C) with a polynomial of sufficient degree, and use Newton-Raphson's method to compute approximate optima of the fits. Note that, as smaller values of β (and β^*) indicate longer intensive searches, a shift towards shorter intensive searches is observed as group sizes increase and resources become more clustered (see text).

group of foragers for different levels of resource clustering. These results indicate that, when the environment displays little clustering (for $\gamma = 1.5$, Fig. 3.5A), competition for resources is low and foraging efficiencies for all studied values of N are the same. In contrast, when resources become more clustered as γ increases, dependence of the group search efficiency on group size becomes apparent. When γ increases while group sizes are large, on-patch competition becomes more fierce, and as a result the optimal value for β is larger compared to when group sizes are smaller

(Fig. 3.5D). This indicates that group members benefit from shortening their intensive searches, as patches are perceived to hold less resources since more competitors are destructively feeding on the patch as well. The fact that optimal strategies differ significantly depending on group sizes is a clear indication of the effect of competition over the same set of resources.

3.3.2.3 Distribution over resources consumed

As previously mentioned, when computing the group search efficiency as the group average, this average does not always reflect the underlying distribution of resource encounters. In reality, resource intake distributions become increasingly skewed towards the lucky few who detected dense patches early in the foraging task when resources are significantly clustered (see Appendix 3.B, Fig. 3.B.1). We note that a log-normal distribution describes the individual resource intake distribution well, as long as environments are not significantly clustered ($\gamma \lesssim 1.5$). However, the log-normal distribution fails to describe resource intake rates when resources are more clustered for $\gamma \gtrsim 2$ (Fig. 3.6E and Fig. 3.B.1), making direct comparison between the group average and the mean of the distribution inaccurate. The significant probability for a forager to find little to no resources becomes apparent as γ increases, and subsequently increases the empirical variation (standard deviation) over resource intake rates (Fig. 3.7B).

The skewed distribution further provides an explanation for the previously mentioned shift towards shorter intensive searches. Recall that $\gamma \approx 3$ results in highly clustered resource distributions, often consisting of a single, large patch. Since foragers not on that patch greatly benefit from shorter intensive searches on smaller patches (recall Fig. 3.1D), by shortening their intensive searches they increase the likelihood to find the largest patch and thereby profit the most. Additionally, due to the fact that switching back from the intensive search to the extensive search is modulated by the distance wherein no targets have been detected, the effects of β diminish as patches become increasingly dense, as is the case for large enough γ . Therefore, the foraging task effectively reduces towards detecting the largest patch as quickly as possible; a task which is achieved by ballistic motion ($\alpha \rightarrow 1$) and reduced exploitation of suboptimal patches (smaller β).

Furthermore, we note that the rising inequality can be captured by computing inequality measures [110]. We compute Gini coefficients (see Appendix 3.B for more details) and note that as γ increases, so does the Gini coefficient (see Fig. 3.A.2A). More specifically, these high valued Gini coefficients correspond to high inequality in resource intake (thus a large variation). Values of the Gini coefficient are larger when group sizes increase, displaying increased inequality in resource intake rates in larger groups.

3.3.3 A group of foragers with $r > 0$

Next, we introduce more explicit competition by including attraction towards (nearby) conspecifics within a specific attraction radius r . Recall that foragers are attracted to others within this radius, but only if the focal forager is in the extensive search mode and the other forager (the attractor) is in the intensive search mode. This adapts the bimodal Lévy search from the previous sections to a trimodal one. Intuitively, when each forager assumes the underlying resource landscape to be clustered, joining others in the vicinity is essentially similar as a bout of guided motion towards an existing patch, making joining an effective strategy in sparse, patchy resource landscapes. Therefore, the effectiveness of such opportunistic joining behavior depends heavily on the resource landscape, resource availability, joining ranges and individual decision processes.

In all experiments where attraction is introduced we fix our trimodal Lévy search with ballistic extensive searches ($\alpha = 1.1$) and sufficiently long intensive searches ($\beta = 10^{-4}$) such that joining becomes feasible. Recall that β modulates the duration of a foragers being attracted, thus choosing large values of β can result in truncation of attracted bouts due to the attractor exiting the intensive search before the focal forager has joined. This implies to the attracted forager that there are no more resources, hence stopping the attractive bout midway, making attraction less likely to result in resource detection. Moreover, we are interested in finding quantitative criteria for which joining becomes beneficial based on resource clustering and resource availability. Obviously, when the durations over which individuals can be attracted decrease, the system converges to a system of solitary foragers, and results will converge to those presented above for $r = 0$. Therefore, we omit short lengths of attraction by choosing β such that time ranges over which foragers can effectively join nearby neighbors are sufficiently long. A more intricate study on the effects of β on the effective joining range is considered to be out of the scope of this work.

3.3.3.1 Competition and the group search efficiency

We compare the trimodal Lévy search with the bimodal one by computing the relative group search efficiency

$$\eta_r = \frac{\eta_N(r > 0)}{\eta_N(r = 0)}, \quad (3.7)$$

where η_N is the group search efficiency from the bimodal search with $r = 0$ as in Eq. (3.6), and $\eta_N(r)$ the same group search efficiency of the trimodal group of foragers, but with attraction radius $r > 0$. Values of $\eta_r > 1$ define joining as being beneficial, where $\eta_r < 1$ makes individual strategies (i.e. the bimodal search) more efficient.

We plot the relative group search efficiency for a clustered resource landscape versus the joining range in Fig. 3.6A. We note that small populations of foragers have a wide range of γ over which joining is beneficial,

due to the relative local abundance of resources when joining successful conspecifics. When group sizes increase, joining becomes less beneficial due to fast, local depletion of patches due to the destructive nature of the foraging. More specifically, optimal joining ranges (insets Fig. 3.6A,B) decrease significantly as groups grow larger, indicating that joining others is only beneficial if local resource availability is sufficient.

Additionally, we plot the relative search efficiency at a fixed value of r against γ and N in Fig. 3.7B, where we would like to emphasize again that N directly influences the relative resource availability. As expected, if there is no significant degree of clustering ($\gamma \lesssim 2$), joining strategies are disadvantageous regardless of relative resource density. The reason is that joining others becomes highly inefficient as patches consist of few resources, thereby resulting in attracted foragers arriving at an already depleted patch. This effectively wastes search time, where the individual would have been better off by ignoring the successful forager in favor of an explorative search. In contrast, when resources become increasingly clustered, we see that joining others increases the group search efficiency depending on the relative resource availability. Larger groups need more clustered resource landscapes ($\gamma \gtrsim 2.5$) in order for joining to be group beneficial than smaller groups ($\gamma \gtrsim 2$).

To further differentiate between the effectiveness of joining others versus continuing individual exploration, we plot the relative effectiveness of the explorative mode(s) of the bi- and trimodal Lévy searches. For the bimodal Lévy search with $r = 0$, we record the efficiency of the extensive search η_e . For the trimodal Lévy search, we combine the extensive search with parts of the foraging task over which the forager is attracted to a successful conspecific, which effectively captures all non-intensive search modes, into η_s . By plotting the ratio of these efficiencies in Fig. 3.6C, we see that joining others increases the efficiency of non-intensive searches significantly. For joining ranges $r/L \approx 0.1$ we note that exploration with joining others can be more than twice as efficient than individual exploration, but only when group sizes are not too large ($N = 64, 128$). When group sizes grow too large, the efficiency of joining others decreases, again due to increased levels of intraspecific competition.

3.3.3.2 Joining promotes intake equality

While attraction to successful conspecifics might not always maximize the groups search efficiency defined in Eq. (3.6), it is important to note that the distribution over resource intake equalizes as the log-normal distribution becomes a better fit (Fig. 3.6E, Fig. 3.B.1), and variation in resource intake rates decreases (Fig. 3.6F). This is also reflected by the Gini coefficients, as they decrease when attraction is introduced compared to a system of non-interacting foragers (Fig. 3.A.2B,C). It is further substantiated by noting that the group average, the expected value of the search efficiency and the mode are closer to one another as joining ranges increase

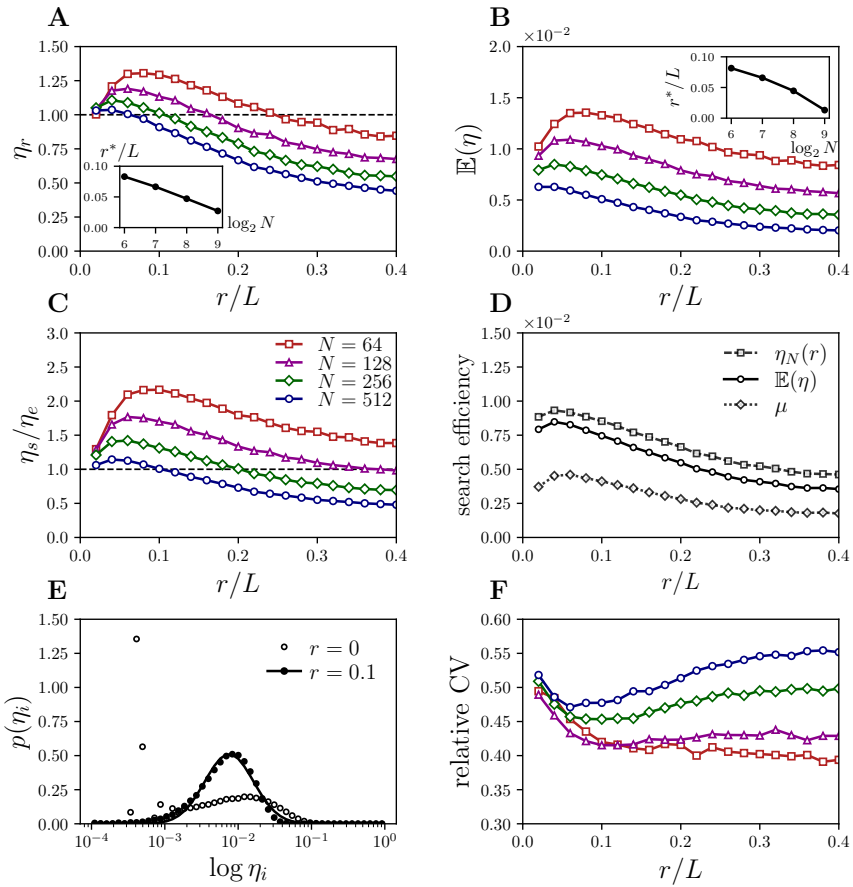


Figure 3.6: Influence of the joining range on several metrics. Foragers executed bi- or trimodal searches, with fixed $\alpha = 1.1$ and $\beta = 10^{-4}$, in a clustered resource landscape with $\gamma = 2.5$. (A) The relative search efficiency η_r versus the joining range for different relative resource densities modulated by group size N . (B) The expected value of the log-normal distribution over search efficiencies versus the joining range. (C) Relative efficiency of joining η_s/η_e versus the joining range (see text). (D) Differences between group averaged search efficiency $\eta_N(r)$, expected value from the log-normal distribution $\mathbb{E}(\eta)$ and the mode μ , versus joining range for $N = 256$. Discrepancies between expected value and mode increase with increased inequality in resource intake. (E) Change in distribution of individual search efficiencies η_i when joining ranges are introduced, with $r = 0.1$. The black line is a log-normal distribution fitted to the data. Note that for $r = 0$ a log-normal distribution does not appropriately describe the underlying distribution and can therefore not be fitted (see text). (F) Relative coefficient of variation (CV) versus the joining range.

(Fig. 3.6D). Full equality of these different metrics would be obtained by a normal distribution, however we found no evidence for intake rates being normally distributed. We further observe the empirical standard deviation to be decreasing when joining ranges are introduced, as becomes visible when plotting the relative coefficient of variation (CV) in Fig. 3.6F. Most interestingly, while the relative CV is strictly smaller for any $r > 0$ than for $r = 0$, we note that for large group sizes the CV increases as joining ranges increase. This results directly from longer joining ranges being counterproductive, as distant arrivals at depleted patches become increasingly common (see the above discussion on group search efficiency). This illustrates that, while any joining range decreases the variation in resource intake, there exist optimal joining ranges that facilitate the smallest coefficient of variation.

Overall, these results imply the following: joining others reduces variations in individual resource intake rates, i.e. increases group equality, *regardless* of the joining range. We wish to emphasize that while joining others from far away might not be optimal due to the increased costs of traveling, it does result in more foragers finding at least something, hence the group of foragers resorts to a *low mean, low variance* strategy, cf. [17]. Finally, we mention that joining ranges should not be too short, as the system then converges to the non-interacting system for which results are as discussed in Section 3.3.2.

3.3.4 When is joining beneficial for group foragers?

To arrive at a quantitative explanation of when joining is beneficial when foraging in groups, we have to ask what constitutes beneficial search strategies. Intuitively, a group benefits when each individual benefits, but individuals can benefit from group-level interactions while not increasing group search efficiency. The main example to illustrate such behavior is survival. In principle, survival rates are tightly interconnected with the search efficiency, where higher (group) search efficiencies should result in higher survival rates. However, when the threshold for survival is relatively low, i.e. foragers do not need to optimize but just need to achieve a minimum number of resources in order to survive, foragers benefit from others simply by avoiding starvation. This, as mentioned above, can be achieved by reducing the variation in resource intake rates, since individuals rely on others for locating patches rich in resources [14, 17, 26, 111]. In such cases, while the group might not act optimally, the survival probability of individuals increases, which provides an ulterior incentive that might motivate joining others as an attractive strategy.

In order to study when individuals within a group benefit from joining others, we need to quantitatively determine under what environmental conditions individual strategies are less effective than group-level strategies. In Fig. 3.7A, we show the regions over which joining others be-

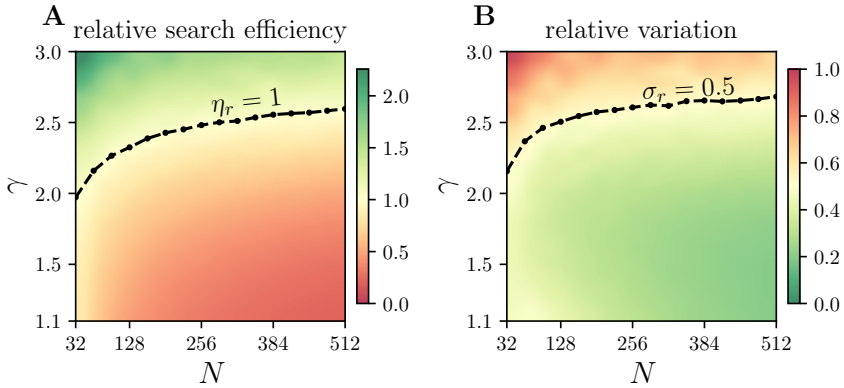


Figure 3.7: Benefits of joining nearby conspecifics for different resource landscapes γ and relative resource density facilitated by group size N . Search strategies are fixed bi- and trimodal Lévy searches with $\alpha = 1.1$, $\beta = 10^{-4}$ and $r/L = 0.1$. (A) The relative search efficiency η_r computed through Eq. (3.7). Dashed line depicts $\eta_r = 1$, where joining becomes group efficient above this line ($\eta_r > 1$), and individual strategies (ignoring conspecifics) are preferred below ($\eta_r < 1$). (B) The relative variation of the search efficiency, expressed as the relative empirical standard deviation. Lower values of σ_r indicate lower variation of intake rates during the foraging task. Importantly, joining others *always* reduces variation in resource intake rates for any $r > 0$ (see text). Note the contrast with (A), indicating that regions where group efficiencies fall are regions with lowest (relative) variance. Dashed line at σ_r serves as a guide to the eye, where the variation is half of a non-communicating group. Results are obtained by averaging over 100 different realizations for each combination of N and γ .

comes beneficial based on increased average search efficiencies. Individuals within large groups only achieve higher average search efficiencies when environments are significantly clustered for $\gamma \gtrsim 2.5$, while in contrast small groups of foragers benefit from joining others (and others joining) for $\gamma \gtrsim 2$. The resource landscape that results in the largest increase in group search efficiencies are obviously those who are highly clustered for $\gamma = 3$ (and subsequently $\gamma \geq 3$ as well), since resources can only be found in a single, dense patch.

On the other hand, reducing the variation in order to avoid starvation follows a completely contrasting trend. In Fig. 3.7B, we see that the relative variation decreases as environments become less clustered, and when group sizes increase. Thus, effective survival probabilities might increase since individuals are more likely to find the minimum number of resources necessary for survival. Thus, whether foragers at the individual level benefit from joining others in a specific environment with some fixed level of fractality, depends critically on the current needs of the individual.

What do these results imply for group foraging strategies in fractal resource landscapes? These quantitative results show that multimodal searches increase the individual search efficiency given that the resource distribution is sufficiently clustered. This implies that individuals benefit from approximating the local resource density and change their diffusion rates accordingly. These adaptive strategies are still beneficial when the single forager is a member of a larger group of foragers within the same resource landscape. As group search efficiencies decrease due to rising inequalities in resource intake, groups (as well as most individuals) benefit from joining ranges within which successful foragers will effectively share the detected resource with nearby others. However, as joining ranges increase, so does the level of intraspecific competition and thereby the efficiency of joining bouts, as patches become more likely to be depleted upon arrival. The optimal joining range depends heavily on the relative resource availability, as larger group sizes facilitate joining to be beneficial only if the environment is sufficiently clustered (Fig. 3.7A). As a result, we argue that foragers should be able to approximate both local resource density and conspecific density, and adapt their search strategies accordingly, if they are to forage efficiently.

3.4 Discussion

In this work we have introduced an agent-based model where individuals execute a trimodal Lévy search that consists of three distinct modes. The first mode defines an explorative Lévy search with a fixed Lévy parameter α . The second mode is triggered upon resource detection and defines local exploitation by an exhaustive-like Brownian search with $\alpha = 3$. The third mode considers attraction to successful conspecifics within a radius r , where the behavioral change upon resource detection by the other forager acts as public information that can be exploited by others. Thus, foragers who are currently executing an intensive search can serve as attractive conspecifics due to each forager assuming the resource distribution to be clustered to some degree.

By quantitatively determining the benefits of joining others compared to a system where joining was not included, we illustrated a wide range of efficient multimodal Lévy searches that depends critically on the resource distribution and relative resource availability. In this work, we considered resource-to-resource distances that follow an inverse power law distribution that generates fractal resource landscapes. We have shown that in a system of non-interacting foragers, implicit intraspecific competition as foragers compete for a limited set of resources, results in skewed distributions over resource intake levels when resources are significantly clustered. Moreover, while more scattered resource distributions result in resource intakes to follow a log-normal distribution, we showed that the variation in resource intake rates grows as resources become increasingly clustered.

When introducing the possibility of joining successful nearby others, a group of foragers displayed more equalized resource intake distributions. We showed that this resulted in resource intake rates being log-normally distributed over the entire studied range of resource distributions.

Our model illustrates that small groups of foragers can benefit from joining others by increasing the average search efficiency, over a wider range of resource distributions than large groups, as larger groups experience higher levels of intraspecific competition. However, individuals within a group do not necessarily need to optimize group-level search efficiencies, but should rather ensure minimal resource intake in order to survive. By introducing joining ranges we showed that variation in resource intakes decreased, regardless of the spatial distribution and availability of resources. The reduction in variance was maximized in environmental conditions where relative group search efficiencies were lowest, displaying that the benefits of joining conspecifics strongly depend on the ulterior motive of each individual. Thus, our quantitative approach reinstates that foraging behavior need not necessarily facilitate optimality by increasing average search efficiencies, but might rather increase survival rates by decreasing variation in resource intakes.

Whereas we have studied the influence of a static switching parameter β , more intricate adaptive strategies are observed in natural systems [21]. For example, β can be adapted based on the number of nearby foragers, resembling quorum responses [112, 113] and consensus models [114, 115]. While such group-level responses correspond more to a collective system rather than a competitive system, they are of importance to engineering artificial systems such as swarms [105, 116]. In this context, we have studied homogeneous groups wherein each individual commits to the same strategy, however within-group heterogeneity exists and is widespread across different organisms [5, 104, 117–119], and as a result artificial systems as well [120, 121]. Precisely how such within-group differences of individual needs and preferences shapes both individual and group behavior is still largely unknown.

In this study, we have purposely left out investigations into the diffusion characteristics of the resulting motion of foragers. Since attraction towards successful others truncates long Lévy flights, the resulting random search might not have flight lengths sampled from a power-law distribution [122, 123], but rather follow different, less diffusive, distributions [54]. Such truncated Lévy searches have been studied in the context of attraction [6] and memory [80]. Furthermore, diffusion characteristics, and thereby foraging efficiencies, are highly influenced by the resource landscape [73]. A more thorough investigation into the walk characteristics of individuals in the information sharing framework is therefore required.

Additionally, we wish to address that our model does not include a spatial memory component that foraging individuals often possess [80, 109, 124–126], where intricate memory models were observed in multi-

ple species such as bees [127], flower bats [128], and Capuchin monkeys [129, 130]. We do wish to note that the distance in which no resources have been detected used in the decision process (as in Eq. (3.3)), serves as an extremely primitive memory model that considers foragers that approximate local resource densities (see also [50, 131]). Although in our experiments more explicit spatial memory is not beneficial due to the destructive nature of the foraging process, more intricate resource regeneration patterns might provide benefits of more intricate memory components [132].

Finally, we should note that foraging benefits – as discussed in Section 3.3.4 – are not expected to be the only driving forces behind group formation [5]. For example, group size might increase foraging success [10, 133], or a minimum group size is required when taking down large prey [134, 135]. In contrast, hierarchical structures that increase competition might lead to individuals spreading out when resources are scarce [136]. Furthermore, as foragers themselves might be subjected to predation, increased group sizes can reduce the individual predation risk while foraging [137–141]. Moreover, predation, or a general exposure to risk of dying, is seemingly tightly connected with landscape fragmentation [142–144]. As an effect, larger groups often exhibit higher survival and reproduction rates than smaller groups [145, 146]. Within the context of our model, as lower levels of resource fractality mediated by low values of γ result in grouping to be disadvantageous, thus most likely leading to decreased group sizes. Hence, our model appears to suggest that increased resource fragmentation can negatively impact survival and reproduction rates, a result which can have profound ecological consequences. Therefore, while individuals might forage more efficiently alone, survival related aspects outside of resource intake are likely to be a driving force behind group foraging as well and can greatly impact the survival of foraging species and should therefore undoubtedly be included in future models.

In this chapter, we introduced an agent-based model for group foraging in fractal resource landscapes. Depending on group sizes and resource distributions, we have showed that joining others is not necessarily beneficial. However, joining does decrease variation in resource intakes across all levels of fractality, thus possibly impacting survival rates of species foraging in groups. This illustrates that driving forces other than increased foraging efficiency cannot be ignored in future models on foraging in groups.

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Appendices

3.A Influence of β on intensive searches

Recall the switching probability defined in Eq. (3.3) as

$$p_\beta(L_0) = 1 - \exp\left[\frac{-\beta L_0}{\ell_0}\right] \quad (3.8)$$

To further consolidate the effects of β on the expected lengths of the intensive search, we can write the probability of exiting the intensive search after having traveled a distance L_0 without resource detection, as

$$\begin{aligned} \hat{p}_\beta(L_0) &= p_\beta(L_0) \prod_{\ell=\ell_0}^{L_0} \left(1 - p_\beta(\ell)\right) \\ &= \left(1 - \exp\left[\frac{-\beta L_0}{\ell_0}\right]\right) \prod_{\ell=\ell_0}^{L_0} \exp\left[\frac{-\beta \ell}{\ell_0}\right] \\ \text{let } t &= L_0/\ell_0, s = \ell/\ell_0 \\ \Rightarrow \hat{p}_\beta(t) &= (1 - \exp[-\beta t]) \prod_{s=1}^t \exp[-\beta s] \\ &= (1 - \exp[-\beta t]) \exp\left[-\frac{1}{2}\beta(t-1)t\right]. \end{aligned} \quad (3.9)$$

In this form, t represents the (discrete) time, i.e. number of steps, needed to travel a distance of L_0 with increments of ℓ_0 . Then, the cumulative of

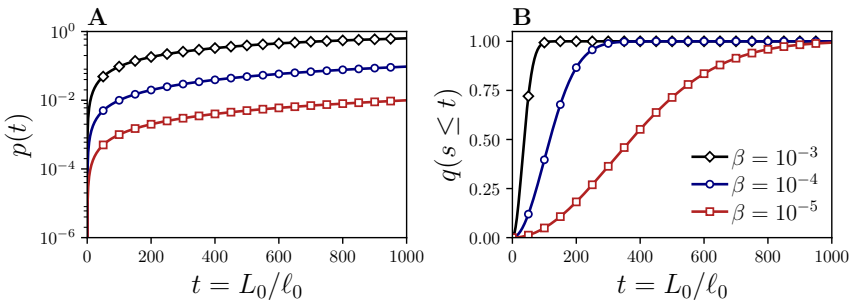


Figure 3.A.1: Plots on the influence of β on the length (number of steps) of intensive searches. (A) Probability of switching from intensive search to extensive search after t steps of no resource detection. (B) Cumulative density function of taking at most t steps until truncation of the intensive search. Note that (relatively) large values of β result in fast truncation of intensive searches, while smaller values facilitate longer intensive searches.

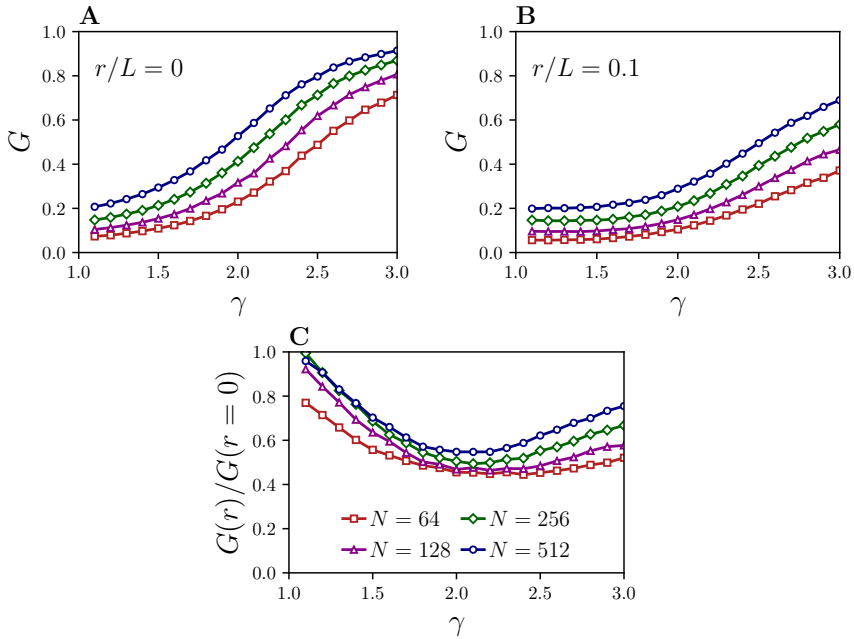


Figure 3.A.2: Gini coefficient G versus the resource Lévy parameter γ , for different group sizes N . (A) G for a group of non-interacting foragers, while (B) includes attraction over a distance $r/L = 0.1$. As illustrated in (C), Gini coefficients are lower overall when attraction is introduced, resulting in a more equal distribution over resource intake (and foraging efficiencies, see also Fig. 3.B.1). Results are obtained for fixed bi- and trimodal Lévy searches with $\alpha = 1.1$ and $\beta = 10^{-4}$.

this distribution defines the probability of needing *at most* t steps before truncation

$$q(s \leq t) = \int_0^t ds (1 - \exp[-\beta s]) \exp\left[-\frac{1}{2}\beta(s-1)s\right]. \quad (3.10)$$

We note that as $t \rightarrow \infty$ we have $q \rightarrow 1$ for any $\beta > 0$, but also $q \rightarrow 1$ as $\beta \rightarrow \infty$ for any $t > 0$. Hence, long distances without resource encounter will (eventually) truncate the intensive search, while $\beta = \infty$ completely removes the intensive search mode since foragers immediately switch back to the extensive search mode at the next step.

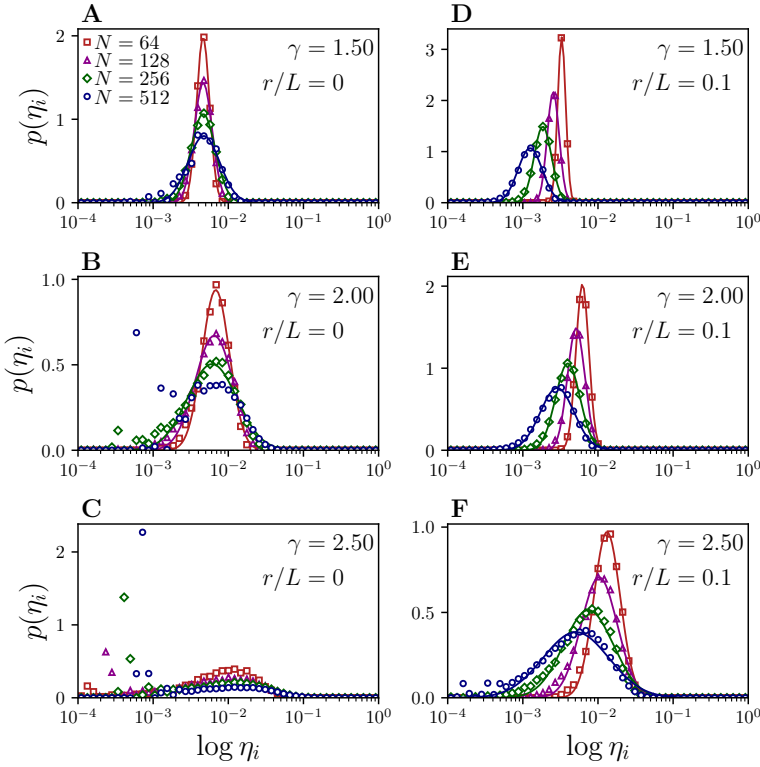


Figure 3.B.1: Distribution over search efficiencies of individuals for different group sizes, in resource landscapes with different levels of clustering (see Fig. 3.1). For each forager i , the search efficiency η_i is computed as in Eq. (3.5), and subsequently the distribution $p(\eta_i)$ can be determined. Solid lines are fitted log-normal distributions, where fits are only displayed if they explain the data points. When resources are not significantly clustered for $\gamma \lesssim 2$, shown in (A) and (D), search efficiencies are log-normally distributed regardless of joining ranges. Furthermore note lower mean search efficiencies as joining ranges are introduced in (D). In (E) and (F), joining ranges result in log-normal distributions when environments are clustered, where the absence of joining ranges skews the distribution due to a large fraction never finding little to no resources visible in (B) and (C). Results are obtained for fixed bi- and trimodal Lévy searches with $\alpha = 1.1$ and $\beta = 10^{-4}$.

3.B Details on the resource intake distribution

Recall that intraspecific competition manifests itself in rising inequality within the distribution of resource intake among foragers (see Sections 3.3.2 and 3.3.3). As a way of measuring this inequality, we use the

well-known Gini coefficient [110, 147], defines as

$$G = \frac{\sum_{i=1}^N \sum_{j=1}^N |k_i - k_j|}{2N \sum_{i=1}^N k_i}. \quad (3.11)$$

Such a measure of inequality has been previously used in ecological frameworks [148]. Essentially, values of $G \rightarrow 1$ represent heavily skewed distributions, where a small subpopulation has access to the most resources. In contrast, values of $G \rightarrow 0$ indicate high equality among group members, where $G = 0$ is achieved when each individual has equal resource intake. We plot the Gini coefficient versus the degree of clustering defined by γ in Fig. 3.A.2A,B. As seen, G increases as the resource landscape becomes increasingly clustered, reinstating that a lucky subpopulation discovers the dense patch early in the foraging process and thereby accounting for the majority of resources consumed. When introducing a joining range of $r > 0$, we note that income inequality decreases through decreased values of G . We additionally compute relative income inequalities by comparing Gini coefficient of groups of interacting and non-interacting groups. Interestingly, intermediate values of $\gamma \approx 2$ seem to promote lowest relative income equality when joining foragers join successful others.

Details of the individual search efficiencies are illustrated in Fig. 3.B.1, where distributions over search efficiencies are plotted for different group sizes and degrees of resource clustering. First, when considering the bimodal group search with $r = 0$, log-normal distributions of resource intake are a good fit only if environments are *not* clustered. When resource distributions become more clustered, the log-normal distribution fails to explain the data due to the existence of a large fraction of foragers finding little to no resources (high G , see Fig. 3.A.2A). When foragers join successful others however, the log-normal distribution provides a good fit over a wide range of clustering degrees. Deviations indicative of a significant proportion of foragers finding little to no resources arise only when resources are densely clustered ($\gamma \gtrsim 2.5$, see Fig. 3.B.1C,F).

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4

Resource ephemerality influences effectiveness of altruistic behavior in collective foraging

Abstract

In the previous chapter, we studied group foraging in a competitive system. However, groups of foragers are not always competitive, but can display collective behavior instead. In this chapter, we shall discuss collective foraging by introducing an agent-based model wherein foragers can exhibit altruism by actively recruiting others to feed on ephemeral patches, instead of exploiting these individually. Such altruistic behavior is only beneficial when recruiters can efficiently locate conspecifics, a condition that is often not met due to the short interaction ranges that many collective systems exhibit. We let foragers assume Lévy searches and show that the recruitment strategies that optimize conspecific encounter rates are those that contrast the dispersal characteristics of conspecifics. Additionally, as patches only persist for some limited time, we show that recruitment is only advantageous for the collective if enough conspecifics are recruited before the patch disappears. Therefore, patches with durations below a certain threshold should not trigger recruitment behavior, while patches that persist for longer should. We examine the effectiveness of such threshold-based recruitment behavior by varying patch ephemerality, and measure the foraging efficiency of the collective system. Our results indicate that active recruitment is beneficial to the collective, but only when patches are scarce and sufficiently persistent. Additionally, we show that collective foraging efficiencies increase when effective forager densities are high, as high densities increase conspecific encounter rates. Moreover, when effective densities are high, we show that a simple passive strategy is much more effective

than active recruitment. However, as many collective systems exhibit short interaction radii, and thus low effective densities, the recruitment scheme presented in this chapter is more likely to be advantageous for realistic collective foraging systems. Finally, we show that choosing suboptimal values has rather limited impact, whereas the choice whether to recruit is critical. This can have profound consequences for future applications in artificial foraging systems, as the results presented in this chapter indicate that complex decisions on patch detection are not required for a collective system to benefit from altruistic behavior.

4.1 Introduction

Collectively foraging for resources is critical to the survival of many animal species. In principle, foraging entails the entire process of searching for resources whose locations within the environment are often unknown. To detect these resources, foragers must resort to random searches. Whereas individual random searches can be optimized over a wide range of environmental constraints [2–6], a collective system can potentially exploit interactions to further increase the foraging efficiency [7–11]. While the impact of foraging efficiency with respect to survival is evident, collective foraging additionally provides an important source of inspiration for designing artificial systems [12, 13]. In general, collective systems rely on possibly intricate communication patterns that are essential to spread information within the system. This is a crucial aspect for the emergence of many types of collective dynamics, with applications ranging from understanding and controlling epidemiology [14, 15] to sensor networks [16–19]. Identifying and understanding essential parts of the decision processes that underlie collective foraging, therefore, proves largely beneficial for designing efficient artificial systems.

Many foraging environments contain ample resources distributed according to fragmented, or patchy, distributions [20–26]. In such systems, locating patches rich in resources is difficult for individuals. Rather obviously, groups and collective systems can benefit from interactions between conspecifics [27], effectively parallelizing the search [28]. Then, for example, by joining successful conspecifics, aggregations on salient patches can occur [29–33]. However, when the number of foragers feeding on the patches increases, foraging efficiencies might fall due to competition for resources on the patches [34]. This on-patch competition introduces an important distinction between groups and collective systems. However, the terms used to describe these inherently distinct systems are often used interchangeably (see e.g., [9, 27], among others).

In particular, we argue that group (or social) foraging should describe groups of foragers wherein individuals do not necessarily display behavior that maximizes group foraging efficiencies. Instead, they often favor individually optimal behavior, as hypothesized by the selfish herd hypothesis [35]. Group foraging has been extensively studied using numerous

decision processes, interaction models, and resource landscapes [9, 36–39]. While it has been observed that grouping provides individual advantages such as reduced predation risk [40–42] and reduced risk of starvation [43, 44], these advantages do not necessarily translate to higher group foraging efficiencies [44–48]. This indicates that it is important to distinguish between individuals living in groups and individuals who are part of a collective, especially in the context of foraging.

In contrast with groups, we argue that collective systems should exhibit traits that aim to maximize collective benefits. This effectively eliminates the on-patch resource competition encountered in group foraging, as it is not a disadvantage that resources need to be shared. As an effect, it allows individuals to instead favor behavior that is advantageous for the collective, but importantly not necessarily advantageous for the individual itself. Such behavior includes altruistic behavior that has been observed in collective systems, such as active inhibition of visitation to exhausted patches [49], optimal task allocations [50–52], and (active) recruitment towards salient patches [51, 53–58], the latter of which is studied in this work.

Benefits of collective behavior depend strongly on resource distribution. Static resource distributions wherein patch locations and their respective qualities are known result in ideal free distributions that optimize foraging efficiencies [59, 60]. However, patch locations and qualities are most often not known. In addition, resource distributions are not static but possess potentially complex dynamics, expressed by resource locations changing over time. Precise resource locations are often tied to seasonality [61], other periodic changes [62], or more complex resource dynamics, possibly leading to random patch durations [63]. Additionally, resource consumption, akin to destructive foraging [64], in combination with spatial characteristics of the resource distribution, can lead to ephemeral resource aggregations [9, 65, 66].

Patchy and ephemeral resource landscapes imply that full global information, e.g., global knowledge about salient patch locations, is not necessarily beneficial for a collective system [67]. For example, if the information on patches rich in resources is disseminated across vast distances, it is highly likely that these patches have already disappeared once the information reaches eligible conspecifics. Moreover, when rapid decision making is concerned, lower levels of connectivity are preferred [68–70]. These types of collective systems have also been observed in swarming animals, where social interactions were purposely limited to enhance collective responses [71–74]. Despite the obvious disadvantages, highly connected systems that facilitate global information dissemination have been extensively studied in the context of group and collective foraging (e.g., [9, 10, 75]). Additionally, previous work has studied the effect of (static) topological networks, such as scale-free networks [10, 76–79]. However, foraging systems with reduced information dissemination caused by short communication ranges have not been thoroughly discussed, even though these limitations

are encountered in many artificial collective systems [80–84].

In this work, we study collective foraging in patchy and ephemeral resource landscapes wherein foragers can only interact with conspecifics over short distances. We study altruistic systems with active recruitment, as foragers that have detected a patch can choose to recruit others over individually exploiting the resources on the patch. Such recruiting schemes have been mostly observed in ants [51, 53, 55–57] and bees [54, 58] and embody the underlying premise of a collective system: altruism. Note that since the individual that detected the patch does not consume resources itself, recruitment represents pure altruistic behavior. It carries similarities with resource sharing [79], which, besides in swarming insects, has been observed in social mammals such as primates [85] and wolves [86]. Obviously, and as we shall show, recruitment should only be viable if the expected net gain of the collective is positive [87]. In other words, when patches are ephemeral, and the recruiter does not encounter conspecifics before the patch disappears, it would have been better – both at the individual *and* collective level – if it had individually exploited the patch. Therefore, at patch detection, each forager needs to assess whether the patch is of sufficient quality to deem recruiting others as efficient behavior.

To make this decision, we argue that each forager needs to be able to estimate conspecific encounter rates. In this work, we show that under some reasonable assumptions, encounter rates can be estimated, by which individuals can decide whether to recruit or not. When designing artificial systems, these estimates can be given as prior information. More specifically, we shall show that our model effectively describes a threshold foraging model [39, 87, 88], where only patches above a certain threshold provide a positive gain by recruiting others. Following observations from natural systems [89], we consider ephemeral resource landscapes wherein the patches containing resources have durations sampled from an inverse power law. By studying different levels of resource ephemerality and resource availability, we show that recruiting others increases collective foraging efficiencies, but only if patches are both difficult to locate and persistent. Thus, our results show that altruistic behavior can decrease foraging efficiencies when patches are readily available or when patches persist over time scales shorter than those over which others can be recruited. Additionally, while we present a rudimentary scaling analysis that reveals optimal choices of thresholds, we show that precise computation of these thresholds is not necessary for altruistic behavior to be beneficial. Interestingly, the choice of whether to recruit at all is a far more important decision. Finally, we show that the benefits of recruitment depend strongly on forager density and communication ranges. More specifically, simple group strategies, which are not necessarily altruistic, can outperform collective strategies when random conspecific encounter rates are high, which occurs when forager density is high. This illustrates the complexity of the

decision process that individuals within a collective might undergo, as the most efficient strategy can critically depend on the many variables present in the system.

4.2 Model description

4.2.1 Environment description

We model our environment as a two-dimensional area of dimension $L \times L$ with periodic boundaries. This design reflects environments that are much larger than the individual and allows us to study the macroscopic properties of the collective in isolation of more invasive boundary effects. Within the environment, we spatially distribute M patches uniformly. We couple patch quality and patch duration by assuming that higher quality patches are available for longer times. This assumption is largely based on the fact that foragers spend more time in high quality patches than in low quality ones [90–95], as foraging in patchy environments is often understood as an evidence accumulation process [96–98]. We let the duration of a patch τ follow an inverse power law with parameter γ as

$$p(\tau) = \begin{cases} A\tau^{-\gamma} & t_{\min} \leq \tau \leq t_{\max}, \\ 0 & \text{otherwise,} \end{cases} \quad (4.1)$$

where $A = (\gamma - 1)/(t_{\min}^{1-\gamma} - t_{\max}^{1-\gamma})$ a normalization constant. Note the lower truncation at t_{\min} that indicates patches exist at least for some period of time. As we are interested in realistic ephemeral landscapes, patches should not be of extremely long (potentially infinite) duration, as ensured by the upper truncation at t_{\max} . These scale-free, inverse power law distributions have been widely observed in natural systems [65, 89, 99–101]. In the asymptotic limit of $t_{\max} \rightarrow \infty$, we have for $\gamma \rightarrow 1$, that the patch distribution is rather broad, implying that patches of almost all possible durations will appear within the environment. In contrast, when γ increases the inverse power law loses its heavy tail and converges to a normal distribution for $\gamma \geq 3$. Most notably, for $\gamma \gg 1$, the environment consists of patches of duration t_{\min} , since the probability of patches of longer duration appearing becomes negligible in practice. In order to preserve overall statistical properties of environments patch density is kept constant throughout the experiments by respawning a new patch at a random location each time a patch disappears (see below).

We assume patches to be of infinite capacity, but of finite duration, as to model an ephemeral landscape wherein short-term (over) consumption does not deplete patches. While this assumption might appear counter-intuitive, systems wherein (small) groups of individuals cannot fully exhaust ephemeral patches are widespread [63]. Examples are bats preying on insect swarms [102] or fish [103, 104], whales foraging on seasonally

available krill [105, 106], birds feeding on vast swarms of insects [107], and fish feeding on mobile prey [108]. Moreover, having (potentially) infinite patch density, but limited patch availability, effectively captures effects similar to patch exhaustion due to resource consumption. It allows us to model ephemeral resource landscapes without having to take into account short-term resource competition on the patches.

We should mention that the spatial distribution of resources (and subsequently the patches wherein they reside) often follow fractal distributions [9, 24, 65, 66] (and see Chapter 3), where intra-resource distances are distributed according to an inverse power law similar to Eq. (4.1). However, fragmented environments wherein resources are contained in uniformly distributed fixed size patches are observed in natural systems as well [109, 110] and subsequently extensively studied in the context of foraging [4, 10, 89, 111, 112]. Since we focus on large-scale systems, we omit more complex within-patch resource distributions and dynamics by assuming that times between subsequent resource encounters are negligible. This assumption allows us to study the (dis)advantages of collective behavior in isolation of other, possibly intrusive, effects. We consider more detailed spatial resource distributions and dynamics to be out of the scope of this work.

4.2.2 Individual behavior

We consider a homogeneous collective system of N foragers. Each individual forager is able to detect patches within a detection radius $R \ll L$. Foragers are able to observe patch duration (i.e. patch quality) instantaneously. They can interact with conspecifics within an interaction radius $r > R$ (but $r \ll L$, see Appendix 4.A). More specifically, we focus on interaction ranges below a critical value $r < r_c$ as values above this critical value result in fully connected communication networks. Fully connected networks enable formation of global information, whereas information is most often locally bound in collective systems (see Appendix 4.A for a more detailed discussion). Additionally, we consider foragers with constant velocities (see below).

We discretize time into steps of fixed size, initialize foragers uniformly, and have them explore the environment using a Lévy walk. Recall that Lévy walks have been extensively studied in foraging literature as recent advances in data logging techniques highlight them as efficient random searches when patches (or resources) are sparsely distributed [2, 65, 113–115]. Whereas the robustness of Lévy walks in a foraging context has been widely established [4, 5, 64, 66, 111], it is currently debated whether animals truly execute Lévy walks [116–119]. Despite the ongoing debate, many empirical foraging studies have established the existence of Lévy walks in natural systems (see, e.g., [120–122]).

Lévy walks are characterized by having flight lengths sampled from an

inverse power law with parameter α , i.e.

$$p(\ell) = \begin{cases} Z\ell^{-\alpha} & \ell_0 \leq \ell \leq L, \\ 0 & \text{otherwise,} \end{cases} \quad (4.2)$$

where ℓ_0 is the minimum step size, L the environment size, and $Z = (\alpha - 1)/(\ell_0^{1-\alpha} - L^{1-\alpha})$ the normalization constant. Lower and upper truncation ensure that displacements occur on spatial scales that are relevant to the problem [119]. After sampling a flight length, foragers move in a straight line, with fixed step size (velocity) ℓ_0 , until its full length has been traversed. The travel angle is randomly sampled between 0 and 2π . Note that convergence of the above inverse power law towards a Gaussian process is ultraslow, hence the general characteristics of Lévy distributions are conserved throughout the collective foraging process [123].

In the limit $L \rightarrow \infty$, Lévy walks encompass several distinct modes depending on the Lévy parameter α . These modes characterize spatial displacement and range from ballistic (straight line) motion for $\alpha \rightarrow 1$, to anomalous diffusion for $1 < \alpha < 3$, and normal diffusion (Brownian motion) for $\alpha \geq 3$. As Lévy walks encompass several distinct modes of diffusion they serve as a useful tool from a more practical perspective. Due to their simplicity and robustness for maximizing foraging efficiencies in sparse resource landscapes they have been applied extensively in artificial systems (see e.g., [11, 124–126]). For a more detailed description of Lévy walks and their characteristics we refer the interested reader to more detailed descriptions (e.g., [114, 115]).

While searching the environment, foragers can encounter both patches and conspecifics. A rudimentary scaling analysis (Appendix 4.B) shows that, in order to maximize group search efficiencies, the decision at patch detection is equal to a threshold decision model [39, 87, 88]. Thus, on encountering a patch, individual foragers commence to recruit conspecifics when the (remaining) duration τ exceeds a threshold τ_c . Interestingly, we find that heavy tailed patch distributions drastically reduce the necessity for choosing optimal thresholds (see Section 4.3.3). In other words, while individual decisions can follow a threshold model, the binary decision whether to recruit is more impactful than following a strategy with a precise threshold value.

Inspired by Bartumeus et al. [127], we consider active recruitment to be a random search as well, but for conspecifics instead of patches. We let recruiting foragers additionally follow a Lévy walk, but with a different parameter α' . Diffusion of individuals within our system of foragers will therefore be described by a vector $\alpha = (\alpha, \alpha')$, where α is the parameter for the random search and α' for the recruiting search. The goal of recruiting is to encounter conspecifics and subsequently communicate the location of the previously detected patch. Then, encountered conspecifics travel to the advocated patch and proceed to feed on the resources residing on the

patch. To facilitate this, the recruiting forager has access to a simple, finite-length memory component wherein the location and the duration (quality) of the patch are stored. Note that memory formation occurs only at patch detection. The recruiting forager effectively acts as an advocate for the patch and induces ephemeral aggregations of multiple foragers onto the patch. More specifically, since we consider interaction radii larger than the patch detection range ($r > R$), recruiters effectively enlarge patch detection ranges such that others, that would otherwise not be aware of the patch, can benefit (and subsequently the collective as a whole).

Individual foragers apply the following set of rules, given a prior threshold τ_c :

- (i) When detecting a patch, if $\tau > \tau_c$, try to recruit others by executing a Lévy search with parameter α' . Recruiting stops when the time needed to travel towards the advocated patch exceeds the remaining duration of the patch.
- (ii) When detecting a patch, if $\tau \leq \tau_c$, stay and feed on the patch by continuously consuming resources with rate ϵ . Feeding stops when the patch disappears.
- (iii) When detecting a recruiting conspecific, travel towards the advocated patch and, once on the patch, feed with rate ϵ until the patch disappears.
- (iv) When neither a patch nor a recruiting conspecific is detected, continue the Lévy search with parameter α .
- (v) This rule pertains to the regeneration of patches once depleted. After the duration τ of the patch has been expired, the patch is replaced by a new patch at a random location with a new duration sampled from the inverse power law with parameter γ (see Eq. (4.1)). Thus, the total number of available patches M remains fixed.

Note that once a patch has been detected, only the forager that first detected it will try to recruit others. As a result, recruited foragers in (iii) proceed to feed on the patch and not subsequently start recruiting as well. While more complex systems most likely do not display such binary modes of behavior, we assume a more simplified model as to keep our numerical approach and the accompanying scaling analysis tractable. Furthermore, information on patch duration and location is forgotten after the patch has disappeared, thus memory duration, and subsequent recruiting behavior, has finite lengths. Finally, while flights can be truncated upon both patch and conspecific detection, we do not study (group) diffusion characteristics in this work. A more thorough investigation in potential crowding effects, by additionally taking finite-size effects into account, is warranted when one aims to implement our model in more realistic artificial systems, or when studying different scales over which foraging takes place.

4.3 Results

We study a system of $N = 256$ foragers in the $L \times L$ environment with $L = 1000$. We consider equal step size and patch detection radius $\ell_0 = R = 1$ and normalize consumption rate $\epsilon = 1$. Interactions with conspecifics can occur when the distance is smaller than $r = 0.0375L \approx \frac{1}{2}r_c$ (Appendix 4.A). While the interaction radius and forager density influence the metrics that will be presented, we found that general characteristics did not change when properly accounting for the number of foragers (but see the discussion on density-related effects in Section 4.3.4). Patch durations are distributed according to the inverse power law with minimum duration $t_{\min} = 10$ and maximum duration $t_{\max} = L/\ell_0 = 1000$. While the minimum patch duration ensures patches exist at least for some time that they can be detected, the maximum duration is fixed at L/ℓ_0 as we assume patches for which recruiting distances can be longer than the environment size unrealistic. Unless mentioned otherwise, we compute statistical averages over 250 different foraging instances of duration $T = 10^5$ steps.

4.3.1 Conspecific encounter rates

Let us first briefly discuss a non-interacting group of N foragers foraging in an ephemeral landscape. This is achieved by considering both $\tau_c = \infty$ and $r = 0$. Such systems define group foraging in a selfish system where foragers do not take others into account. Patch distribution and patch ephemerality define a destructive foraging instance for uniformly distributed targets for which it is known that the optimal Lévy parameter $\alpha_{opt} \rightarrow 1$ [2, 3, 66]. In other words, ballistic motion provides the highest patch encounter rates and therefore the highest search efficiencies.

When foragers are able to interact with conspecifics ($\tau_c \leq t_{\max}$, $r > 0$) we also expect the patch detection rate to be maximum for $\alpha_{opt} \rightarrow 1$. Hence, recruiters should aim to choose α' to accommodate the highest possible encounter rates *with conspecifics* who execute Lévy walks with $\alpha \rightarrow 1$. Previous work on Lévy searches for dynamic targets who were executing Lévy walks with a different parameter concluded that the most contrasting diffusion optimized search efficiencies [127], i.e. $\alpha'_{opt} \geq 3$ as $\alpha \rightarrow 1$, or vice versa. However, we study forager densities higher than those studied by Bartumeus et al. [127]. Additionally, we consider a different timescale as patches are of (relatively) short and finite duration ($T \gg t_{\max}$). Therefore, recruiters need to encounter conspecifics within a relatively short time scale, which contrasts with the long time scale discussed in Bartumeus et al. [127]. Finally, we study perception ranges for conspecifics to be larger than detection ranges for patches (i.e., $r > R$), while these ranges are equal in Bartumeus et al. [127], as they focus on predator-prey type relations between foragers and resources.

To study what parameters maximize the number of encounters we introduce the conspecific encounter rate ζ as an analogue to the target search

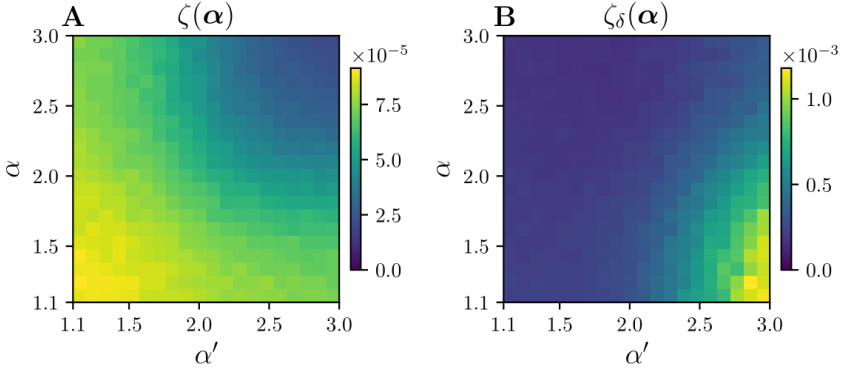


Figure 4.1: Conspecific encounter rates ζ for systems with a single recruiter and $\alpha = (\alpha, \alpha')$. Encounter rates are obtained for $t = 500$, i.e. in the short timescale $1 \ll t \ll L/\ell_0$ (see text and Appendix 4.B). Recall that α is the stable parameter for searching foragers and α' of the recruiter(s). (A) The encounter rate normalized by the total distance traversed d (see Eq. (4.3)). (B) The encounter rate normalized by the displacement from the patch δ , i.e. $\zeta_\delta = n_e/\delta$ (see Eq. (4.16)).

efficiency [2]

$$\zeta = \frac{n_e}{d}, \quad (4.3)$$

where n_e is the number of unique conspecifics encountered within travel distance d . To study encounter rates in more detail, let us temporarily consider a system of N foragers where only a single forager, the recruiter, is recruiting conspecifics. Note that although forager density N heavily influences the rate of conspecific encounters, we found overall characteristics to be similar for different values of N (Appendix 4.C). Results for systems with $N = 256$ are presented in Fig. 4.1A. We see that when $\alpha, \alpha' \rightarrow 1$, conspecific encounter rates are maximized. Note that this contrasts with Bartumeus et al. [127], due to the above described reasons. However, one should be careful not to normalize by the travel distance, as it is actually the displacement from the advocated patch δ that is of importance. If recruiters can recruit others while remaining close to the advocated patch, the efficiency of recruiting should, in principle, be higher. The reason is that encountered conspecifics need not travel long distances to arrive on the patch and are therefore able to feed for longer. As seen in Fig. 4.1B, contrasting strategies with $\alpha' = 3$ as $\alpha \rightarrow 1$ are maximizing encounter rates when normalizing by the displacement (Appendix 4.B). Importantly, encounter rates are maximal when $\alpha \rightarrow 1$. This is desired as ballistic motion provided maximum patch detection rates as well. Therefore, in following experiments, we study systems with fixed $\alpha = (1.1, 3.0)$.

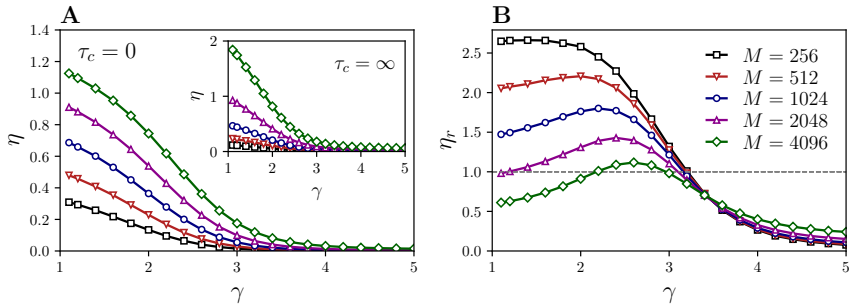


Figure 4.2: Group search efficiency η versus the stable parameter γ for different patch availability M . (A) Group search efficiencies for fully altruistic collective systems ($\tau_c = 0$). Inset displays group search efficiency for individual groups of (selfish) foragers ($\tau_c = \infty$). (B) Relative group search efficiency $\eta_r = \eta(\tau_c = 0)/\eta(\tau_c = \infty)$. Points above the dashed line at $\eta_r = 1$ depict environmental constraints wherein recruitment (altruistic behavior) results in a positive gain in the group search efficiency. Points below the dashed line indicate environments wherein individual searches (selfish behavior) is preferred.

We would briefly like to discuss that, while we have studied Lévy walks with stable parameters $1 \leq \alpha, \alpha' \leq 3$, the above results indicate that the best strategies are those at the extremes of the studied parameter range. Recall that in the asymptotic limit of $L \rightarrow \infty$, these values represent ballistic motion for $\alpha \rightarrow 1$ and Brownian motion for $\alpha' = 3$. Hence, one might argue why we do not study ballistic searchers and Brownian recruiters in favor of more complex Lévy searches with parameters α and α' . We argue that Lévy walks serve as an extremely useful tool to study the influence of movement characteristics, as a single parameter encompasses multiple distinct scales of movement (see Section 4.2.2). Therefore, even though we encounter measures to be maximized at the extremes of the studied parameter range, we argue it is worthwhile to use Lévy walks as the movement model. Finally, when spatial resource distributions are non-uniform, intermediate values of α have been found to optimize Lévy searches (see, e.g., [4, 66, 111]). Hence, using Lévy walks as a prior movement strategy appears appropriate over a wide range of systems as it is both efficient and flexible.

4.3.2 Collective search efficiency

Next, we study collective foraging for homogeneous systems with $\tau_c \geq 0$ and $r > 0$. Note that all foragers can start recruiting others when patch durations exceed the threshold ensuring decentralized behavior typical of swarm systems [81, 82]. To study the foraging efficiency of the collective system, we define the group search efficiency as the average foraging effi-

ciency of its members [9, 11]

$$\eta = \frac{1}{N} \sum_i \frac{k_i}{d_i}, \quad (4.4)$$

with k_i and d_i the number of resources consumed respectively the total distance traversed by forager i .

Let us first discuss two contrasting systems, where one is comprised of purely altruistic foragers with $\tau_c = 0$ and the other a selfish system with $\tau_c = \infty$. Note that when $\tau_c = 0$, all patch detections lead to recruiting behavior, whereas recruiting behavior is never induced for $\tau_c = \infty$. We see in Fig. 4.2 that both the number of patches M and the stable parameter of the resource distribution γ heavily influence both the group search efficiency η and the benefits of recruitment. Fig. 4.3 provides a more detailed view of the effects of γ on distributions over individual search efficiencies η_i .

As γ increases, group search efficiencies for both systems decrease regardless of the value of M . The reason is that resources become increasingly ephemeral and, as such, the search for patches becomes increasingly difficult. This is highlighted by noting that selfish systems with $\tau_c = \infty$ have low search efficiencies as well. Thus, when patch encounters are already rare, a system of collective foragers does not benefit from recruiting as patches are too short-lived to effectively recruit others (Fig. 4.2A). As a result, the relative group search efficiency decreases as γ increases from $\gamma \approx 3$ onward (Fig. 4.2B). This effect is additionally observed in the individual distributions (Fig. 4.3). For low γ , individual efficiencies for altruistic groups are distributed around means higher than for selfish groups. High γ , in contrast, results in systems wherein most individuals consume little to no resources. This effect is exacerbated when M is small (inset Fig. 4.3C).

Search efficiencies increase as γ decreases since patches of longer duration become more readily available. Evidently, larger number of patches result in higher search efficiencies for both selfish and altruistic systems. However, when patches are less numerous, benefits of recruiting others increase for $\gamma \lesssim 3$. In this range of γ , lifetimes of some patches are relatively long due to the dominance of heavy tails in the distribution. If patches are relatively sparse, recruiting others to these rich patches becomes much more beneficial as conspecifics are less likely to encounter patches by themselves. In contrast, when M increases, the relative search efficiency decreases as $\gamma \rightarrow 1$. The reason for this is twofold. First, due to a high number of available resources, individuals are more likely to encounter patches by themselves, reducing the number of ‘free’ foragers (Fig. 4.4A). Here, ‘free’ foragers are those who are eligible to be recruited as they are

¹Note that R^2 here pertains to the statistical measure, not the square of the patch detection radius R .

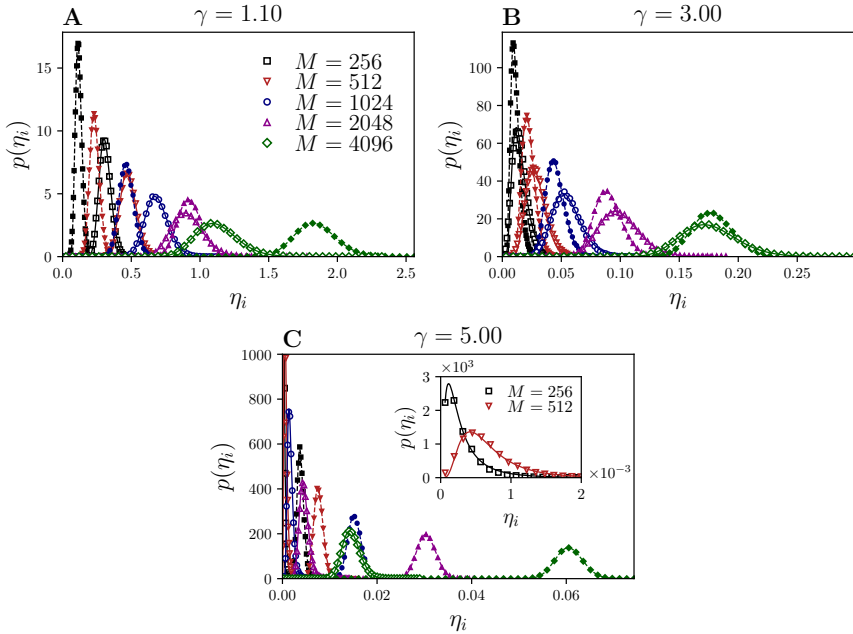


Figure 4.3: Probability density function $p(\eta_i)$ of individual search efficiencies $\eta_i = k_i/d_i$ for different stable parameters γ and resource availabilities M . Empty markers and solid lines indicate altruistic systems with $\tau_c = 0$. Filled markers and dashed lines indicate selfish systems with $\tau_c = \infty$. Lines (both solid and dashed) are fitted log-normal distributions. We found $R^2 > 0.98$ for all fitted curves¹ (see Appendix 4.D and Table T.4.D.1). (A) Density for high resource persistence. (B) Density for intermediate resource persistence. Note that distributions for $\tau_c = 0$ and $\tau_c = \infty$ do not differ significantly for all M , indicating $\eta_r \approx 1$, as expected from Fig. 4.2. (C) Density for low resource persistence. Inset displays details on the (skewed) fitted log-normal distribution for $\gamma = 5$ and $M = 256, 512$.

not feeding, recruiting, or already being attracted, i.e. those who are actively searching for patches. Hence, recruiting instances are less likely to result in patch encounters by conspecifics thereby decreasing the group search efficiency. This is additionally reflected in Fig. 4.4B, as the number of conspecifics per recruit instance decreases as M and γ increase. Second, for large M , the distance needed to travel towards the advocated patch when a forager is being recruited approaches the mean free path λ of the environment. Here, λ indicates the average distance between subsequent patch encounters and its value decreases as M increases. If the travel distance towards the advocated patch approaches (or exceeds) λ , it becomes just as (or more) beneficial to search for patches individually, as is the case for large M (Fig. 4.4C). As a result, altruistic group search efficiencies fall below values of selfish groups.

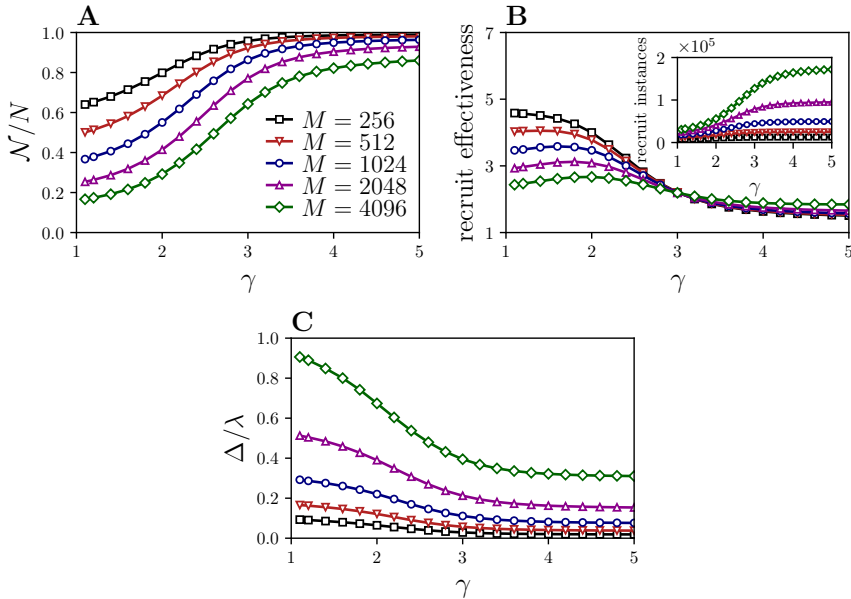


Figure 4.4: Effectiveness of recruiting behavior for an altruistic system ($\tau_c = 0$). (A) Fraction of the number of ‘free’ foragers \mathcal{N} of the total population N at each recruit instance (see text). (B) The effectiveness of recruiting as the total number of conspecifics recruited divided by the total number of recruit instances. Inset displays the absolute number of recruit instances. (C) Average distance needed to travel towards the patch upon being recruited Δ , normalized by the mean free path $\lambda = L^2/2RM$. Environments wherein $\Delta < \lambda$ indicate (potential) benefits of recruiting instances, whereas environments where $\Delta \gtrsim \lambda$ have individual searches equally, to more, efficient than being recruited (see text).

4.3.3 Threshold decision making

Having established that recruitment is only beneficial when patches are sparse and persistent, we would like to discuss effects of the threshold τ_c . Recall that foragers only start recruiting others when the patch duration is higher than a specific threshold τ_c (see Section 4.2.2 and Appendix 4.B). As visible in Fig. 4.5, the effect of the threshold on the group search efficiency is not significant when resource distributions are either fully dominated by the heavy tail ($\gamma \approx 1$), or when the heavy tail is suppressed ($\gamma \gg 1$).

In the former, decreases in search efficiencies become significant as τ_c approaches the maximum patch duration. The reason for this observation is that, when $\gamma \approx 1$, foragers will try to recruit others for (often occurring) patches with long duration regardless. Hence, it does not matter if τ_c is much smaller, and ephemeral aggregations still occur on these long duration patches. Since these aggregations account for a large portion of the to-

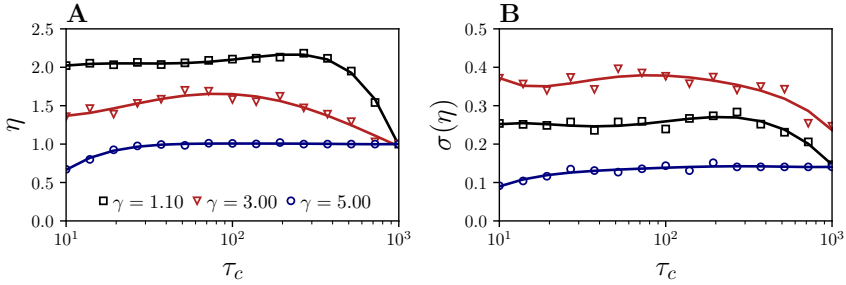


Figure 4.5: Influence of threshold τ_c on the group search efficiency η . Note that $\tau_c = t_{\min} = 10$ corresponds to a fully altruistic system and $\tau_c = t_{\max} = 1000$ to a selfish one. Results are obtained for $M = 512$, but similar results are obtained for other values of M . Lines are a guide to the eye. (A) Normalized group search efficiency η versus the threshold τ_c . Note the optimal value for $\gamma = 3$ at $\tau_c \approx 100$ (see text). (B) The standard deviation of η . Standard deviation is largest when $\gamma = 3$ due to high variation in the resource ephemerality.

tal group search efficiency, the effect of τ_c on η is small as long as $\tau_c < t_{\max}$. Only when τ_c approaches t_{\max} do foragers stop recruiting others to patches with long durations, thereby reducing the group search efficiency.

In contrast, for $\gamma \gg 1$, τ_c influences the search efficiency only when it approaches the minimum patch duration. In this regime, the heavy tails of the inverse power law distribution are suppressed and extremely few patches with durations $\tau \gg t_{\min}$ are present in the environment. Hence, for $\gamma = 5$, we see that when τ_c is sufficiently large to ensure recruiting behavior for (almost) all encountered patches, the search efficiency becomes independent of τ_c . Interestingly, recruiting does not provide a beneficial strategy in this regime anyways, regardless of the choice of τ_c (Fig. 4.2).

More interestingly, effects of τ_c are more pronounced for distributions where the heavy tail is suppressed, but only to some extent, i.e. for $\gamma \approx 3$. Here, we observe an optimal threshold at $\tau_c \approx 100$. Patch durations below this threshold are of relatively small duration such that the expected number of conspecifics encountered in that time is small (Fig. 4.B.1). Hence, the collective is better off by individually exploiting these patches, as trying to recruit others will most likely lead to a negative gain. Patches above this threshold do provide a net gain, which is why search efficiencies are maximized for this precise choice of threshold. However, note that the variation of the search efficiency is additionally maximized for these intermediate values of γ , because variation in resource ephemerality is high when heavy tails are only partially suppressed.

Finally, we would like to emphasize that precise (optimal) computation for τ_c is not a necessity for the collective system to benefit from the described altruistic behavior. As long as patches are difficult to locate (small

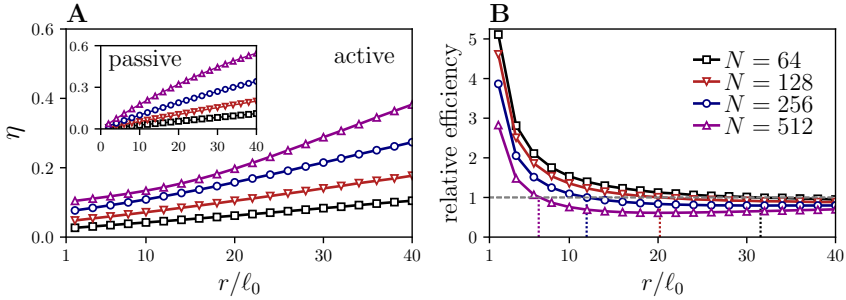


Figure 4.6: Group search efficiencies for active and passive recruiters versus the normalized interaction radius r/ℓ_0 for different forager numbers N . Results are obtained for $M = 256$ and $\gamma = 1.1$ in order to simulate environmental conditions under which recruitment is known to be beneficial (see Fig. 4.2). (A) The group search efficiency η for active recruitment (with $\alpha' = 3$). Inset shows the group search efficiency for passive recruitment (static recruiter). (B) The relative efficiency as $\eta_{\text{active}}/\eta_{\text{passive}}$. Dashed line at 1 indicates the threshold and individual dotted vertical lines indicate interaction radii r' above which passive recruitment becomes more efficient.

M) and persistent ($\gamma \lesssim 3$), recruiting others increases group search efficiencies. This has possible far-reaching implications for designing artificial systems, as these results appear to indicate that prior beliefs do not determine whether altruistic behavior is advantageous or not. Additionally, as priors for more complex collective systems are often difficult to estimate, our results seem to imply that these are not necessary. While more intricate patch or forager dynamics might necessitate more precise threshold approximations, or even updating current beliefs as estimates deviate from their initial values [128–130], we argue that simply always trying to recruit others is an advantageous strategy given that patches are persistent and interaction radii are small.

4.3.4 Effect of forager density on recruitment behavior

Finally, we would like to address the effect of forager density on the effectiveness of active recruitment. While the above results consider systems that actively recruit for conspecifics, searching conspecifics can be informed more passively by having the recruiter remain on the patch while continuously announcing its location to passersby, here called *passive recruitment*. Increased foraging efficiency of such a strategy is implied by noting that, when searching for conspecifics, a recruiter should not stray far from the patch (see Section 4.3.1 and Fig. 4.1). Note that these strategies effectively reduce the system to a group foraging system (see our discussion in Section 4.1), where foragers join successful nearby foragers that have detected a patch (as in, e.g., [9, 38, 87]).

To appropriately compare active and passive recruitment strategies, let us consider an environment with conditions such that altruistic systems (with $\tau = 0$) outperform selfish systems (with $\tau = \infty$). Under these conditions, passive recruitment outperforms active recruitment only when interaction radii are sufficiently large, i.e. $r > r'$ (Fig. 4.6). Here, r' is the interaction radius above which passive recruitment results in higher foraging efficiencies than active recruitment. As N increases and $r > r'$, random encounter rates increase, reducing potential advantages of active recruitment. Furthermore, passively announcing becomes more efficient due to weak decreases in encounter rate (Fig. 4.B.2A) being compensated by strong decreases in total travel distance (Fig. 4.C.1A). Indeed, our results indicate that r' is smaller for higher forager densities (Fig. 4.6B).

For $r < r'$, we find that active recruitment outperforms passive recruitment due to increased recruit efficiencies (Fig. 4.C.1C,D). Here, recruit efficiencies are computed by measuring the number of resources consumed by *recruited* foragers, i.e. it acts as an indication of the remaining time upon patch arrival. Hence, higher recruit efficiencies indicate that active recruitment results in conspecifics arriving earlier on the ephemeral patches, thus consuming more resources per distance traveled when compared with passive recruitment strategies. Moreover, for r small and approaching the patch detection radius ($r \approx R$), we find active recruitment to outperform passive recruitment substantially. The reason for this can be understood when considering that recruitment effectively transforms the search for difficult to detect patches to a search for more easily detectable conspecifics. When interaction radii decrease, it becomes more difficult to detect searching foragers. If $r \leq R$, passive recruitment cannot be considered beneficial as it becomes more likely (or just as likely for $r = R$) to encounter patches than conspecifics. In contrast, active recruitment, while displaying decreased foraging efficiencies as r decreases (Fig. 4.6A), displays higher relative foraging efficiencies compared to passive recruitment. The reason is that the patch itself remains exploitable, while the recruiter effectively simulates an additional patch detection opportunity with some radius $r > R$. In this regime, patch detection can result from detecting the patch itself or by detecting the active recruiter, thus increasing the patch detection probability significantly and leading to higher relative foraging efficiencies.

We would like to emphasize that, while passive recruitment strategies appear enticing due to increased foraging efficiencies for sufficient $r > r'$, many collective systems exhibit small interaction radii. For example, honeybees recruit others by touch [58, 131, 132], i.e. $r \approx \ell_0$. Additionally, scalable collective robot systems exhibit interaction radii that extend only several body lengths [82, 124, 133]. Thus, despite the simplicity of passive recruitment strategies, which one might desire over more complex active recruitment strategies, the above results indicate that active recruitment is more likely to be advantageous for realistic collective foraging systems

with small interaction ranges.

These density related effects display that, while (active) recruitment can be considered beneficial for the collective, the recruitment strategy itself should critically depend on individual and collective variables, such as the interaction radius and the forager density. Further investigation into optimal recruitment strategies is considered to be a topic for future research.

4.4 Discussion

In this work, we have studied a collective system capable of altruistic behavior. Foragers that detected patches could, instead of feeding individually, decide to recruit others to increase the overall resource intake of the collective. We showed that, by coupling patch quality and patch duration, recruiting times of individuals could be estimated by performing a scaling analysis of the underlying Lévy random search. Our analysis showed that this effectively reduces the decision on patch detection to a threshold decision. Patch qualities above this threshold are expected to have a positive net gain when actively recruiting others. Indeed, our agent-based model displayed increased collective search efficiencies, but only when patch ephemerality was not too high and patches were difficult to locate. Moreover, we showed that the influence of the threshold is small compared to the decision of whether to recruit or not. Only when patch ephemerality was intermediate, i.e. when high quality patches appeared sporadically, did a more fine-tuned threshold result in higher collective foraging efficiencies, although increases in search efficiencies were relatively small. Therefore, always recruiting remained a valid strategy that resulted in increased group search efficiencies, potentially alleviating the necessity for individuals to determine optimal thresholds.

We considered patch quality (duration) to be instantaneously available and an objective measure identical for all individuals. Realistically, this assumption does not necessarily hold since patch quality can be subjective or change over time depending on the needs of the individual or the collective [75, 134, 135]. Additionally, satiation might influence individual decisions, as individuals tend to change behavior based on their internal state [136, 137]. Thus, while including yet more crucial pieces of natural foraging behavior into a model might prove difficult, it is critical to understand the decision process that members of a collective undergo.

Furthermore, in this work, we assumed that individuals were only able to communicate over short distances. While we argued that information being only locally available is not necessarily detrimental, studies on natural systems have found that animals can transfer information across potentially large distances [67, 76, 138–140] or form ephemeral groups that can lead to vastly different communication networks [141], such as topological distances [72, 142] or scale-free networks [10, 77, 78]. Further investigation into the ranges over which collective systems can communicate, and the

effect on decision processes, should therefore be considered.

As widely observed in swarming insects, such as ants [143] and bees [144], nest formation can circumvent the lack of long communication ranges. This type of foraging, called *central place* foraging, has been observed in other animal species as well [145–148]. Specifically, it considers individuals that frequently return to a single nesting site whereon all communication takes place. This work studies a system where the spatial forager distribution is essentially uniform and only results in higher forager densities when ephemeral aggregations form on the patches. Although it is known that spatiality affects decision making [149], how exactly different behavior can induce more efficient spatial distributions is not yet fully understood. Nonetheless, we believe that the model presented here may help the design of more efficient artificial systems, as well as potentially help to explain empirical data on collective foraging.

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Appendices

4.A Details on the interaction graph

Here, we aim to get an understanding of the effect of the interaction radius r on the macroscopic behavior of the collective system. Possible interactions between individuals, and thereby their collective behavior, are fully characterized by the resulting proximity graph given this interaction radius. In this interaction graph interpretation, each individual represents a vertex where edges between vertices denote interaction and only exist when the distance between two vertices is smaller than r . The foragers' positions define a random geometric graph albeit that the distribution over time is not necessarily uniform due to the ephemeral aggregations on patches. Below, we illustrate that an initial uniform distribution makes certain values of the interaction radius uninteresting to (artificial) collective system studies.

Let us consider a uniform distribution of vertices (forager positions). Formally, one can define the connectivity (or degree) of a random geometric graph as the average number of connections per vertex:

$$\kappa = 2E/N, \quad (4.5)$$

where E is the number of edges within the graph. Let us furthermore define the size of the giant component to be $NG(\kappa)$, where G indicates the fraction of vertices present in the giant component. It is known that there exists a critical connectivity κ_c for which, in the limit of $N \rightarrow \infty$, we have that $G \rightarrow 1$ for any $\kappa > \kappa_c$ [17]. In two-dimensional systems, the value of κ_c can be numerically computed to be $\kappa_c \approx 4.5$. Even though this behavior formally only holds in the limit of $N \rightarrow \infty$, the phase transition is apparent even at relatively small N (Fig. 4.A.1).

In this work, individual foragers can be thought of as circles within the environment, each occupying an area of $V = \pi r^2$, which is related to the connectivity through

$$\kappa = NV. \quad (4.6)$$

From these equations, we can express the interaction radius in terms of the connectivity

$$\frac{r}{L} = \sqrt{\frac{\kappa}{\pi N}}, \quad (4.7)$$

where we have substituted $r \leftarrow r/L$ to express the interaction radius in terms of the environment size L . From this equation, we can immediately compute the critical radius by simply substituting $\kappa = \kappa_c$, and can therefore extract a critical interaction radius r_c above which the network has a giant component containing all individuals.

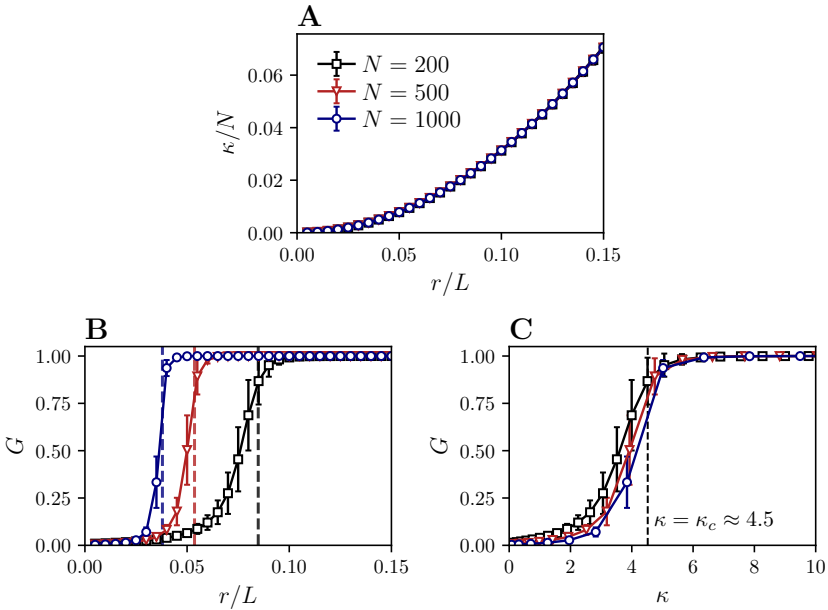


Figure 4.A.1: Numerically computed connectivity κ and giant component parameter G for different vertex numbers N . (A) The normalized connectivity of the resulting random geometric graphs. Note that all vertex numbers collapse onto the same value where $\kappa/N = \pi(r/L)^2$ as per Eq. (4.6). (B) The resulting giant component parameter G as a function of the normalized interaction radius. Dotted vertical lines correspond to the critical radius defined by Eq. (4.5). (C) The same giant component parameter expressed in terms of the connectivity. Note the collapse of the distinct vertex numbers onto the same curve for which any $\kappa > \kappa_c \approx 4.5$ the resulting giant component contains all vertices. In all plots error bars represent 1 standard deviation computed over 1000 separate random geometric graphs.

When the communication network is fully connected, information (e.g. on patch locations) is not locally bound. Therefore, a fully connected network can be assumed to possess global information properties. This regime is out of our current interest, since both natural systems and artificial systems do not possess global information, but instead rely on locally available information to base their decisions on (see e.g., [81, 82]). Therefore, we focus solely on systems with interaction radii $r < r_c$. In particular, we choose $r = \frac{1}{2}r_c \approx 0.0375L$ (see Section 4.3).

4.B Optimal recruitment for Lévy searchers

Below, we perform a scaling analysis and show that the decision to recruit upon patch detection is a threshold decision where patches with qualities

above the threshold result in an expected positive gain and should therefore encourage recruiting. We shall show that the threshold depends on both the forager density, the movement of others, and the range at which foragers can perceive one another.

Let us consider a system of N foragers where one of the foragers detects a patch at time t_0 . Without loss of generality, we set $t_0 = 0$, and the forager has to decide whether to recruit others or exploit the patch individually. Since we consider collective foraging in this study, we assume that successful foragers only start recruiting if the expected net gain by recruiting is positive. Recall (see Section 4.2.1) that the quality of the patch is defined by its (remaining) duration τ . Then, assuming a fixed consumption rate ϵ , we define the net gain g as the difference between individual exploitation and the expected intake rate by recruiting conspecifics:

$$\begin{aligned} g &= -g_{\text{exploit}} + g_{\text{recruit}} \\ &= -\epsilon\tau + \epsilon \int_0^\tau n(t, \boldsymbol{\alpha}) dt, \end{aligned} \quad (4.8)$$

where $n(t, \boldsymbol{\alpha})$ is the expected (average) number of conspecifics feeding on the detected patch at time $t > 0$. Note the dependence on the vector $\boldsymbol{\alpha} = (\alpha, \alpha')$, where α and α' the Lévy parameters of the searchers respectively the recruiter(s) (see Section 4.3.1). The first term in Eq. (4.8) is simply the resource intake for a single forager feeding on the patch. The second term describes the expected number of resources consumed (by others) over the remaining time before the patch disappears. We can rewrite this term by considering the fact that only conspecific encounters up to some time $s(\tau)$ are ‘successful’ encounters, wherein the recruited forager has enough time to still feed on the patch. Thus we find that

$$g_{\text{recruit}} = \epsilon \int_0^{s(\tau, \alpha')} n(t, \boldsymbol{\alpha}) dt, \quad (4.9)$$

where $s(\tau, \alpha')$ depends on the distance the focal forager displaces itself from the detected patch. We would like to emphasize that, for estimating $n(t, \boldsymbol{\alpha})$, one not only needs to consider the expected encounter rate with conspecifics, but also the expected displacement from the patch for the recruiter (Section 4.3.1).

4.B.1 Scaling analysis

The expected time over which the message on the patch location should be disseminated depends on both the remaining time τ and the Lévy parameter of the recruitment search α' . If we consider the focal forager having a displacement $\delta(t, \alpha')$ after some time $t < \tau$, we find that

$$s(\tau) = \tau - \delta(t, \alpha') / \ell_0, \quad (4.10)$$

where ℓ_0 (the step size) the constant velocity of the forager. When assuming time scales are relatively short, i.e. $1 \ll t \ll L/\ell_0$, we know that the spatial moments of the Lévy walk scale as² [150, 151]

$$\langle |x|^k(t) \rangle \simeq \begin{cases} t^{k/(\alpha-1)}, & 1 < \alpha < 3 \text{ and } 0 < k < \alpha - 1, \\ t, & 1 < \alpha < 2 \text{ and } k \geq \alpha - 1, \\ t^{k/2}, & \alpha = 3 \text{ and } k > 0 \end{cases} \quad (4.11)$$

Note that the appropriate timescale wherein the above results hold are applicable to ephemeral landscapes, assuming patch duration is finite and truncated (see Section 4.2.1). One recovers the expected displacement with α' for $k = 1$,

$$\delta(t, \alpha') = \langle |x|(t) \rangle \simeq \begin{cases} t^{1/(\alpha'-1)}, & 2 < \alpha' < 3, \\ t, & 1 < \alpha' \leq 2, \\ t^{1/2}, & \alpha' \geq 3 \end{cases} \quad (4.12)$$

We find our results to match this type of scaling (Fig. 4.B.1A).

The expected number of conspecifics feeding at the patch due to having been recruited can be estimated as

$$n(t, \alpha) \simeq n_e(t - \delta(t, \alpha')/\ell_0, \alpha), \quad 0 < t < s(\tau, \alpha') \quad (4.13)$$

where $n_e(t, \alpha)$ is the expected number of conspecifics encountered within some time t . In other words, the number of foragers feeding on the patch at time t , is approximately equal to the number of encountered foragers at time $t - t'$, with $t' = \delta(t, \alpha')/\ell_0$ the time needed to travel to the patch from distance $\delta(t, \alpha')$. Estimating the number of conspecific encounters requires one to estimate search efficiencies for other Lévy searchers, which to the best of our knowledge has not been done analytically. Numerical simulations reveal linear scaling $n_e \simeq t$ for all values of α that we have studied (Fig. 4.B.1B), and subsequently $n \simeq t$ (Fig. 4.B.2A). A more thorough analytical scaling analysis is considered to be out of scope of this work.

Having established how conspecific encounter rates scale, let us consider the conspecific search efficiency (see Section 4.3.2)

$$\zeta(t, \alpha) = \frac{n_e(t, \alpha)}{\ell_0 t} \quad (4.14)$$

as the number of conspecifics found per distance traveled. It acts as a primer for the choice of α' , i.e. what kind of diffusion should a forager that aims to maximize the number of conspecifics encountered within the remaining patch duration τ . As is known (see e.g., [2, 3]), ballistic motion for $\alpha^* \rightarrow 1$ maximizes the search efficiency in ephemeral landscapes where

²note that here α depicts the parameter for any Lévy search

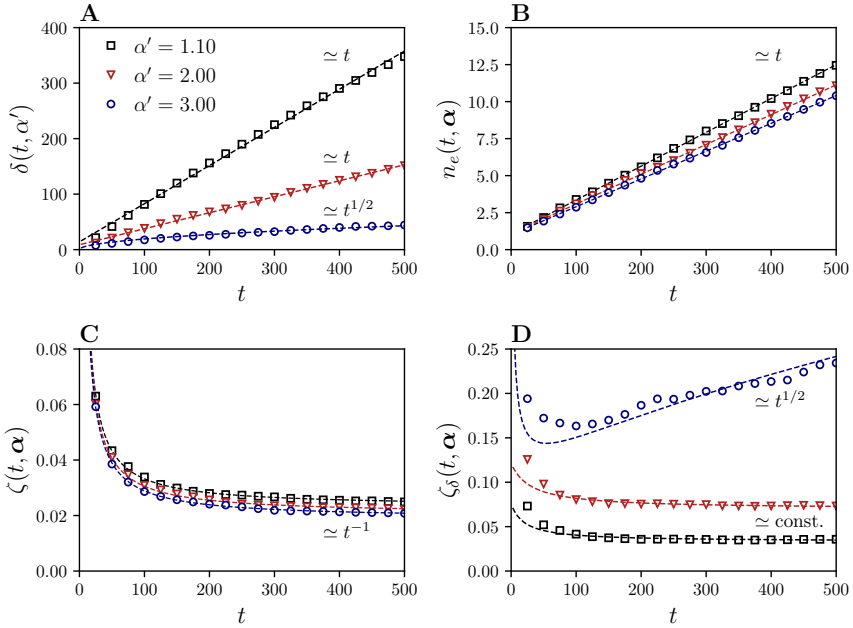


Figure 4.B.1: Scaling analysis of the conspecific encounter efficiency. The appropriate scaling is valid in the asymptotic limit $1 \ll t \ll L/\ell_0$ (see text). (A) The displacement $\delta(t, \alpha')$ from a patch detected at $t = 0$ for different stable recruitment parameters α . (B) The number of conspecifics encountered n_e within a time t for $\alpha = (\alpha, \alpha')$. Here, searchers execute ballistic motion with $\alpha = 1.1$ and recruiters walk with Lévy parameter $\alpha' = 3$ (see text and Section 4.2.2). We find $n_e \simeq t$ for all values of α, α' that we studied. (C) The conspecific search efficiency $\zeta = n_e/\ell_0 t \simeq t^{-1}$ (see text). (D) The normalized conspecific search efficiency $\zeta_\delta = n_e/\delta$. In all figures, dashed lines are fits obtained with non-linear least squares analysis. Scaling of the quantities with time is indicated. Results are obtained by averaging over 250 realizations of an appropriately sized system with $L = 1000$, $N = 256$, $\ell_0 = 1$ and $r = 0.0375L$ (see Section 4.3).

patch locations are uniform. When assuming the remainder of the collective is executing a Lévy search with α^* , we find that a parameter leading to contrasting diffusion, i.e. $\alpha' \geq 3$, optimizes search efficiencies for conspecifics in the short timescale (Fig. 4.1). Using this and the above scaling analysis for the displacement and expected number of encountered conspecifics, we find $\zeta(t, \alpha) \simeq t^{-1}$ (Fig. 4.B.1C).

However, recall that we are not interested in the number of conspecifics encountered per distance traveled, rather as a function of the displacement

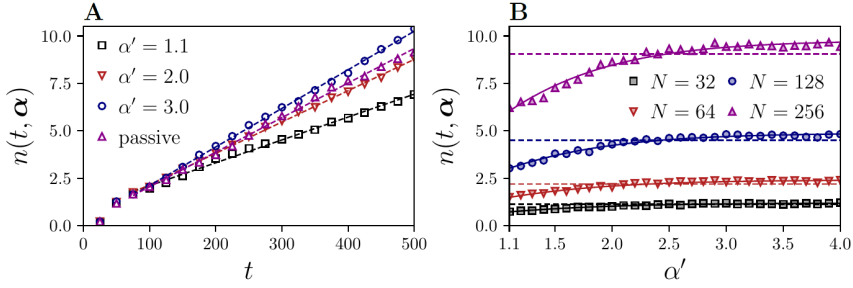


Figure 4.B.2: (A) The number of recruited conspecifics feeding on the patch at time t for different Lévy parameters α' and passive recruitment (static recruiter, see Section 4.3.4). Dashed lines are linear fits with non-linear squares analysis. Averages are obtained over 250 realizations. (B) The expected number of conspecifics feeding on the patch due to having been recruited, $n(t, \alpha)$, as a function of $\alpha = (\alpha, \alpha')$ with fixed $\alpha = 1.1$. Different colors indicate different forager densities, as the number of available foragers depends greatly on the patch distribution (Fig. 4.4). Dotted lines indicate passive recruiters, effectively approximating group-like foraging (see Section 4.3.4). Note that for $\alpha' \gtrsim 3$ the number of foragers feeding on the patch displays a plateau due to the Lévy walk asymptotically converging to Brownian motion as per the central limit theorem. Averages are obtained over 1000 realizations for $t = 500$. Lines are a guide to the eye.

from the patch, i.e.

$$\zeta_\delta = \frac{n_e(t, \alpha)}{\delta(\alpha')}. \quad (4.15)$$

The reason being that recruiting conspecifics while close to the advocated patch results in faster exploitation rates, because recruited foragers arrive at the patch earlier. Since we know the displacement scales as $\delta \simeq t^{1/(\alpha'-1)}$ for $\alpha' > 2$ (Eq. (4.12)), and encounters as $n_e \simeq t$, we find the properly normalized conspecific search efficiency scales as

$$\zeta_\delta(t, \alpha^*) \simeq t^{1/2}, \quad (4.16)$$

where $\alpha^* = (1.1, 3.0)$. In contrast, values of $\alpha' < 2$ result in linear scaling of the displacement, $\delta \simeq t$, hence $\zeta_\delta(t, \alpha) \simeq \text{const.}$, i.e. the normalized conspecific search efficiency approaches a constant value as t increases. Our numerical results indeed verify this behavior, as can be seen in Fig. 4.B.1C,D.

The difference in scaling for $\alpha' \leq 2$ and $\alpha' > 2$ explains why the conspecific search efficiency is maximized with contrasting diffusion characteristics ($\alpha' \geq 3$ as $\alpha \rightarrow 1$). While for $\alpha' \leq 2$ the rate of new conspecific encounters approaches a constant value, it grows with $t^{1/(\alpha'-1)}$ when $\alpha' > 2$,

hence resulting in increased ζ (Fig. 4.1B and Fig. 4.B.1D). It additionally raises the question if different strategies, such as simply announcing while remaining on the patch (i.e., $\delta = 0$), might be more efficient. We compare active recruitment via Lévy walks with a passive strategy in Section 4.3.4 and below in Appendix 4.C.

4.B.2 Threshold decision making

Here, we wish to illustrate that the foragers can be equipped with an effective threshold for which patches with qualities above this threshold should have an expected positive net gain and thus should trigger (active) recruitment. As a result, our model effectively resembles a threshold model, where recruiting others occurs only when the forager expects the collective to benefit (see Section 4.2.2). Recall that we assume that foragers can estimate the optimal recruiting time $s(\tau, \alpha')$ for a given patch duration τ by estimating its displacement following the above scaling analysis. As the coefficients of both the displacement and the number of conspecifics encountered can be numerically computed, we can pre-compute $s(\tau, \alpha')$ from Eq. (4.10) and Eq. (4.12), and subsequently the expected net gain from Eq. (4.8), $s(\tau, \alpha')$ and Eq. (4.13). Since $n(t, \alpha) \simeq t$, we can write $n(t, \alpha) = d_1 t + d_2$. Then net gain g becomes

$$\begin{aligned} g &= -\epsilon\tau + \epsilon \int_0^{s(\tau, \alpha)} n(t, \alpha) dt \\ &= \epsilon \left(\frac{1}{2} d_1 s^2(\tau, \alpha) + d_2 s(\tau, \alpha) - \tau \right), \end{aligned} \quad (4.17)$$

where we have simply integrated the linear approximation of $n(t, \alpha)$. By determining the coefficients, which in artificial systems can be computed beforehand (i.e. be assumed prior knowledge to the forager), one can find critical durations for which $g(\tau_c) = 0$, $\tau_c > 0$. Existing numerical schemes, such as the Newton-Raphson method, can be applied to find these roots.

Then, at patch detection, foragers should recruit when $\tau > \tau_c$ and exploit individually when $\tau \leq \tau_c$. Therefore, advantages of collective behavior depend heavily on the distribution over patch durations (see Section 4.3.2). The threshold τ_c ensures that foragers are not recruiting others towards patches that are not worth the effort and therefore serve as a filter on the individual level. In turn, thresholds greatly simplify decisions of recruited foragers, since instead of a (potentially complex) decision they should simply always travel towards the advocated patch.

We would like to emphasize that our results (see Section 4.3.3 and Fig. 4.5) appear to indicate that the specific choice of threshold does not significantly influence the resulting group search efficiency. This is possibly an artifact of the ephemeral patch distribution that we study here. Hence, different patch distributions might result in more precise estimations of τ_c .

to be far more beneficial for recruiting foragers than the one studied in this work.

4.C Density effects

Forager density affects patch encounter rates and subsequently the number of recruit instances. As a result, passive strategies can become more beneficial (increase foraging efficiency) as interaction radii increase (Section 4.3.4). Note that, despite the apparent increase in foraging efficiency, active recruitment result in more conspecific encounters than passive recruitment (Fig. 4.B.2). Therefore, we compare active and passive recruitment in more detail to investigate when passive recruitment might be more efficient.

To this end, we study a system of N foragers in environmental conditions wherein altruistic recruitment ($\tau = 0$) outperforms selfish systems ($\tau = \infty$). This is realized for persistent patches ($\gamma = 1.1$) and low patch densities ($M = 256$), as indicated in Fig. 4.2. In such environments, we observe that total travel distances are lower for passive recruitment, as the passive recruiter is always on the patch ($\delta = 0$). In contrast, active recruiters increase the distance towards the patch (as $\delta \propto t^{1/2}$, see Section 4.B and Fig. 4.B.1) and thereby increasing distances towards the patch upon recruitment. Note that total travel distances increase with the interaction radius as expected. The (small) decrease for high forager densities as r increases results from the approximately uniform forager distribution on patch detection, leading to instantaneous attraction at distances shorter than r . This induces an overall reduction in the total travel distance.

While larger distances towards the patch seem counter-productive, as the search efficiency is inversely related to the travel distance (Eq. (4.4)), simulations reveal that foraging efficiencies are higher when actively recruiting, but only when interaction radii are sufficiently small (Fig. 4.6). The reason is twofold. First, the recruit effectiveness is larger for active recruitment (Fig. 4.C.1B) as the encounter probability is higher for active recruiters than passive recruiters (Fig. 4.B.2A). Second, for sufficiently small interaction radii, the *recruit efficiency* is larger when actively recruiting conspecifics. The recruit efficiency is computed by the number of resources consumed after being recruited, divided by the total distance traveled, and is shown in Fig. 4.C.1C,D. When actively recruiting, conspecifics arrive on ephemeral patches earlier than when passively recruiting, thus increasing the total number of resources consumed on the patch before it disappears (see also Section 4.3.4).

The benefits of active recruitment depend strongly on the forager density and their interaction radius, because, when interaction radii are sufficiently large, advantages of active recruitment disappear. Travel distances in systems with passive recruitment decrease, due to the recruiter not moving and decreased distances towards the patch upon being re-

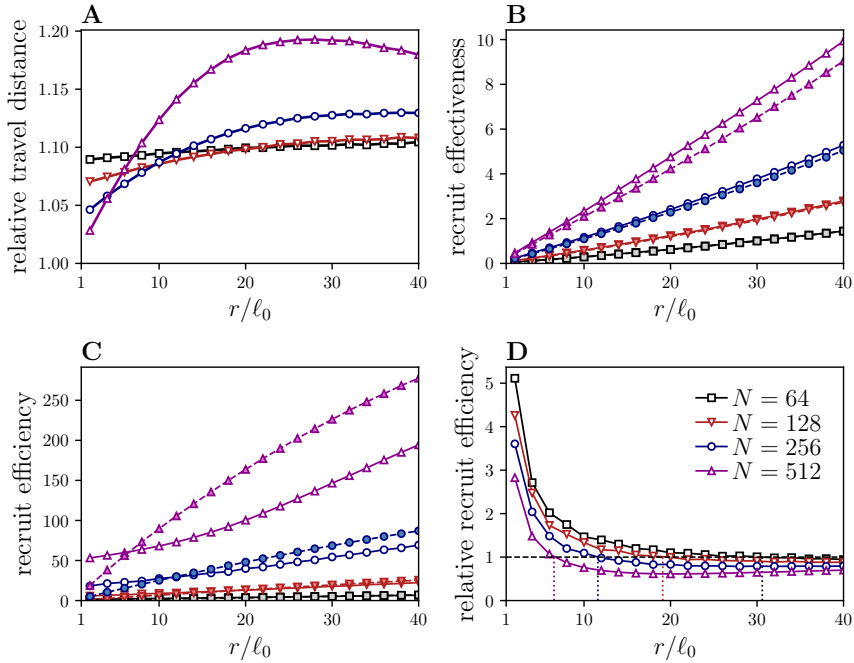


Figure 4.C.1: Comparison of the effect of forager density on the effectiveness and efficiency of recruitment between active and passive recruitment strategies. Results are obtained for $M = 256$ and $\gamma = 1.1$ in order to simulate environmental conditions under which recruitment is known to be beneficial (see text and Fig. 4.2). Solid lines indicate active recruitment with Lévy walks with $\alpha' = 3$ for searching foragers with $\alpha = 1.1$. Dashed lines in (B) and (C) indicate passive recruitment. (A) Total relative travel distance, computed by dividing total travel distance $d = \sum_i d_i$ for active recruitment by total travel distance for passive recruitment. Note that relative travel distance is always greater than 1, indicating that passive recruitment carries lower total travel distances (see text). (B) The recruit effectiveness as the total number of conspecifics recruited divided by the total number of recruit instances. (C) The recruit efficiency as the total number of resources consumed divided by the travel distance (see text and Section 4.3.4). (D) The relative recruit efficiency as the recruit efficiency of active recruitment divided by the recruit efficiency of passive recruitment. Dotted vertical lines indicate interaction radii above which passive recruitment has higher recruit efficiencies than active recruitment. Note that interaction radii for which this occurs are (approximately) equal to those where the forager efficiency indicates similar effects (Fig. 4.6).

cruited (Fig. 4.C.1A), hence increasing the foraging efficiency. This effect is amplified when forager densities are high, resulting in active recruitment being only beneficial when interaction radii are smaller than several body lengths (see Fig. 4.6B, Fig. 4.C.1D and our discussion in Section 4.3.4).

4.D Fitting of the distribution over individual search efficiencies

To measure distributions over individual search efficiencies presented in Fig. 4.3, we numerically compute histograms by computing search efficiencies for each individual forager and attributing them to 50 logarithmically spaced bins between $\eta_i = 0$ and $\eta_i = \eta_{max}$. Here, η_{max} is the greatest measured individual foraging efficiency encountered during our simulations for a specific parameter setting and can be empirically determined.

For generating the fits of the individual search efficiencies in Fig. 4.3, we use non-linear least squares to fit a log-normal distribution to the empirically obtained histograms using the SciPy Python package [152]. To measure the statistical accuracy of the fitted curves, we compute the coefficient of determination R^2 , and found $R^2 > 0.98$ for all curves shown in Fig. 4.3 (Table T.4.D.1).

$\gamma = 1.1$			$\gamma = 3$			$\gamma = 5$		
M	$R^2_{\tau=0}$	$R^2_{\tau=\infty}$	M	$R^2_{\tau=0}$	$R^2_{\tau=\infty}$	M	$R^2_{\tau=0}$	$R^2_{\tau=\infty}$
256	0.996	0.999	256	0.999	0.986	256	0.998	0.998
512	0.998	0.999	512	0.999	0.993	512	0.999	0.992
1024	0.999	0.999	1024	0.999	0.996	1024	0.999	0.998
2048	0.999	0.999	2048	0.999	0.998	2048	0.999	0.999
4096	0.999	0.999	4096	0.999	0.999	4096	0.999	0.999

Table T.4.D.1: R^2 values for fitted log-normal distribution shown in Fig. 4.3 for all shown values of γ and M . $R^2_{\tau=0}$ corresponds to altruistic (collective) systems that always recruit and $R^2_{\tau=\infty}$ are for selfish (group) systems without interaction (see Section 4.3.2).

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5

Foraging behavior and patch size distribution jointly determine population dynamics in fragmented landscapes

Abstract

In all previous chapters, we did not consider the finite lifetime of foragers. Obviously, natural systems exhibit birth and death processes and populations of foragers are nearly never of fixed sizes, but instead fluctuate. These so-called *demographic fluctuations* depend strongly on the foraging behavior of species that, in turn, depends on characteristics of the resource distribution. Critically, population sizes influence the resource distribution as well, bringing about a complex interaction between population dynamics and the landscape configuration. In this chapter, we focus on environments that are, or are becoming, increasingly fragmented, as patches are becoming smaller and more spatially separated. Such fragmentation effects are often the result of habitat loss and present a major threat to the longevity of animal populations. Whereas it is well-established that habitat loss itself negatively affects biodiversity, fragmentation *per se*, i.e. the spatial configuration of habitat, additionally affects population dynamics and ecosystem stability. Within these landscapes, movement between fragments has been put forward as critical to species persistence. However, how optimal foragers respond to the process of fragmentation, and how these adaptations subsequently induce changes in habitat configuration has been largely ignored. To this end, we develop a spatially explicit predator-prey model and study how fragmentation, foraging behavior and demographic rates influence species persistence in fragmented landscapes. In this model, foragers and resources represent the predators and prey, respectively. We study fragmentation by restricting prey to inhabit spatially separated fragments

while, in contrast, predators disperse using Lévy walks and thus induce demographic fluctuations by traveling in between fragments. Our results show that both dispersal rates and fragmentation jointly influence population stability. Increased fragmentation reduces the range of demographic parameters that result in stable coexistence states, thereby suggesting a stronger selective pressure on foraging behavior. Moreover, our results indicate that local prey populations can go extinct, as they are highly sensitive to demographic fluctuations. Because prey is sessile, habitat regeneration is further inhibited by fragmentation, thereby resulting in irreversible loss of habitat. Our results indicate that habitat loss is exacerbated in highly fragmented systems, as smaller fragments are more prone to local extinction events. However, our results also indicate that predator dispersal can reduce, but not prevent, loss of habitat, emphasizing the critical role of dispersal for ecosystem stability in fragmented landscapes.

5.1 Introduction

Habitat fragmentation typically results from habitat loss [2] and results in decreased sizes and increased spatial separation of habitable zones [3, 4]. However, there is a subtle, but distinct, difference between fragmentation resulting from habitat loss and fragmentation *per se*, and the effects of the former and the latter on population dynamics and biodiversity should be discussed separately. As it is well-established that fragmentation induces changes in demographic rates and drifts in population genetics [5, 6], it is therefore critical to assess effects of fragmentation *per se* on population dynamics and ecosystem stability.

In general, fragmentation *per se* (hereafter; fragmentation) has weaker effects on biodiversity than habitat loss [7]. It has been suggested that positive effects of fragmentation are just as likely as negative effects (e.g., [8, 9], but see [10]). Theoretical and experimental studies indicate that fragmentation could favor species persistence by increasing immigration rates, patch connectivity, and habitat diversity (for a review, see [11]). Negative effects, however, are that fragmentation results in increased frequency of local extinction events due to demographic fluctuations and inhibition of regenerative processes, as species become restricted to inhabit only the (small) fragments [12–14]. However, whether, and how, fragmentation impacts population persistence strongly depends on the spatial geometry of the landscape [15, 16]. Furthermore, whereas dispersal of organisms is crucial for the longevity of populations, especially in fragmented landscapes [17, 18], how species respond to and possibly induce changes in habitat configuration has been largely ignored.

On the one hand, studies regarding optimal foraging behavior consider short time scales and assume no demographic events. Instead, they focus on determining a relationship between movement characteristics, search times, and correlations between population and resource density [19]. Individual movement is often modeled using scale-free random searches,

known as Lévy walks, wherein displacement lengths are sampled from inverse power laws with varying exponent [20]. This particular choice of random walk originates from observations that reported scale-free characteristics in movement in different species [21–25]. In general, Lévy walks optimize foraging for sparse resource landscapes [26–29], including fragmented landscapes [30, 31].

On the other hand, studies regarding population dynamics regard longer time scales and often assume simplified movement of individuals [32, 33]. Few studies have integrated optimal foraging behavior into population-based models, and, to the best of our knowledge, only one study has additionally incorporated spatial heterogeneity [34]. However, they did not discuss potential effects of spatial structure of fragmented landscapes. Here, we address such effects by using techniques from landscape ecology that allows for the generation of lattices with varying degrees of fragmentation [35, 36].

To study the interplay between foraging behavior, landscape fragmentation and population dynamics, we develop a spatially explicit predator-prey model. In this model, predators and prey are represented by foragers and resources, respectively. Prey individuals are restricted to inhabit spatially separated fragments, whereas predators are regarded as optimal foragers and thus disperse following a Lévy walk. By varying habitat fragmentation and predator dispersal, we quantitatively investigate the role of dispersal and its effects on ecosystem stability.

5.2 Model description

We develop a stochastic predator-prey model in a two-dimensional landscape with fragmented prey habitat. The landscape is represented by a square lattice of which only a fraction $\rho \in [0, 1]$ of the sites provide prey habitat. To investigate how predator movement and the spatial distribution of prey habitat jointly determine predator-prey population dynamics, we fix the amount of prey habitat ρ and vary the statistical properties of patch size. These statistical properties are determined by the spatial correlations in the distribution of prey habitat. We generate fragmented prey habitat using neutral landscape models [37], which have previously been used to study landscape connectivity and its effects on dispersal (e.g., [38–40]). We generate lattices with periodic boundary conditions from an underlying fractional Brownian motion (fBm) characterized by the Hurst exponent $H \in (0, 1)$, which controls the spatial correlation between adjacent sites [41]. More specifically, we generate lattices of two-dimensional fBm generated by means of spectral synthesis (see, e.g., [41–43]). In general, for $H \rightarrow 0$, adjacent sites are not correlated, resulting in landscapes with several small fragments (high fragmentation). In contrast, $H \rightarrow 1$ signifies high correlations between adjacent sites, thus generating few large fragments (low fragmentation). As we are interested in landscapes with a

specific habitat density ρ , we transform the fBm lattice into a binary lattice by selecting ρL^2 sites with the highest values of fBm to belong to the inhabitable fragments, while the remaining sites are uninhabitable for prey (the matrix). Typical landscapes using this method are illustrated in Fig. 5.1.

It is important to note that fragmentation effects are weaker when habitat density is high (as apparent in Fig. 5.A.1). This is further exemplified by noting that increased fragmentation decreases average patch sizes, as smaller patches become more frequent as H decreases, while large patches become (near) nonexistent (Fig. 5.1B). We consider landscape connectivity to be defined by percolation as the probability p of fragments connecting to either side of the lattice. For large ρ we find $p \rightarrow 1$ regardless of the value of H (Fig. 5.1) and as such, the largest patches contain most of the available habitat, effectively reducing our predator-prey model to one without habitat restrictions for prey (i.e. an homogeneous landscape, as in, e.g., [44, 45]). However, recall that we are interested in the effects of optimal foraging behavior. As such, we examine here landscapes with low habitat density $\rho = 0.2$ as percolation theory predicts disconnected patch structures for all values of H in this regime (see e.g., [38], and Fig. 5.A.1), defining predator dispersal – thus foraging behavior – as a critical component driving population dynamics. Moreover, as Lévy foragers maximize foraging efficiencies only when resource (prey, thus habitat) densities are low

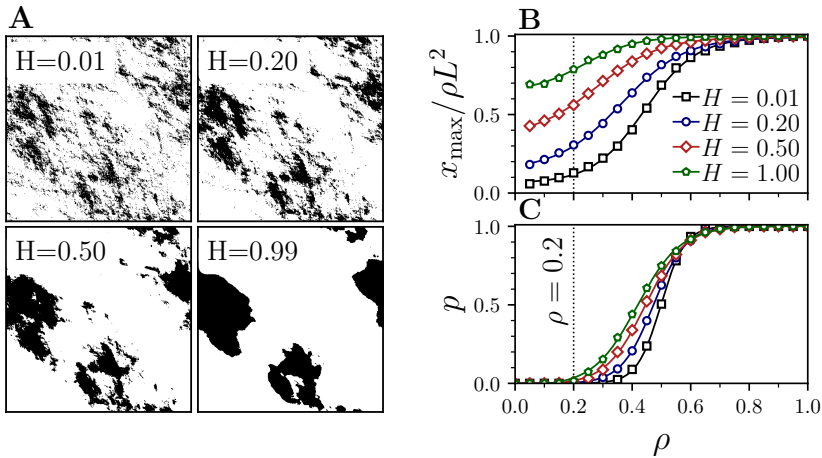


Figure 5.1: (A) $L \times L$ fragmented landscapes of prey habitat used in our model implementation with $L = 512$. Habitat density $\rho = 0.2$ and fragmentation increases with the Hurst exponent, H . Black and white regions depict prey habitat and matrix, respectively. (B) Normalized maximum patch size x_{\max} for different H versus habitat density ρ . (C) Percolation probability p as a function of ρ . Dotted vertical line indicates the habitat density below the percolation threshold ($p \approx 0$) used in our experiments $\rho = 0.2$.

[26], only in landscapes with ρ small would one expect foragers to diffuse anomalously.

5.2.1 The stochastic lattice Lotka-Volterra model

We study a stochastic lattice Lotka-Volterra model (SLLVM) wherein prey habitat is restricted due to the effects of fragmentation, as they cannot inhabit any site belonging to the hostile matrix. Prey is sessile and thus cannot disperse between the spatially separated fragments, whereas predators are allowed to disperse freely and therefore can travel in between fragments. Each site within the lattice can either be empty (\emptyset), contain a predator (X) or prey (Y), or both (XY). Multiple occupation (i.e., XX or YY) is not allowed outside of the predator-prey coexistence state. We consider systems that have the following state transitions with corresponding rates:



where $\tilde{D}, \tilde{\mu}, \tilde{\Lambda}, \tilde{\lambda}, \tilde{\lambda}', \tilde{\sigma}$, the predator dispersal (diffusion) rate, predator death rate, predator-prey interaction rate, predator reproduction rate, predation rate and the prey reproduction rate, respectively. Note that predator death represents a single-site reaction, whereas all other processes describe nearest-neighbor two-site reactions.

The above stochastic model describes the time evolution of a predator-prey system subjected to demographic fluctuations. We define the spatially averaged predator and prey densities N and M as the number of predators and prey per unit area, i.e. $N = n/L^2$ and $M = m/L^2$ with n and m the number of predators and prey on the lattice with L^2 sites. We identify two simple stationary fixed points of interest, namely the two *extinction fixed points*. First, the zero-abundance fixed point $(N, M) = (0, 0)$ where both predator and prey have gone extinct. This fixed point results from overconsumption of prey by predators, which leads to prey and subsequently predator extinction. Second, the prey-proliferation fixed point $(N, M) = (0, \rho)$ where only predators have become extinct. This stable state is an effect of underconsumption that leads to predator extinction,

followed by prey proliferating on the available habitat due to lack of predation. Other stable coexistence fixed points with $N, M > 0$ exist when predators neither over- nor underconsume (Fig. 5.2).

5.2.2 Monte Carlo simulations of the restricted SLLVM

We consider a Monte Carlo approach for simulating the rates of Eq. (5.1). A single Monte Carlo time step corresponds to selecting all occupied sites once on average. We randomly select occupied sites and subject them to the following rules:

- (*predator death*) If the selected site contains a predator, it dies with probability μ ;
- If the predator survived;
 - (*predator dispersal*) if the adjacent site is empty, move there and continue the current relocation (see below);
 - (*relocation truncation*) if the adjacent site contains a predator, truncate the current relocation and do not move;
 - if the adjacent site contains prey, either
 - * (*double occupancy*) move there, but do *not* interact with the prey with probability Λ ;
 - * (*predator reproduction*) truncate the current relocation, and reproduce by adding a predator that replaces the prey with probability λ ;
 - * (*prey consumption*) truncate the current relocation, and consume (replace) prey with probability $\lambda' = 1 - \Lambda - \lambda$. Upon prey consumption (i.e., no reproduction) the selected site is emptied and the prey is replaced with a predator;
- (*prey reproduction*) If the selected site contains prey, choose a habitable adjacent site randomly, and if the chosen site is empty, place a prey there with probability σ .

Here, μ , Λ , λ and σ are the probabilities for predator death, predator-prey interaction, predator reproduction and prey reproduction respectively. Note that we have $\lambda + \lambda' + \Lambda = 1$, thus prey consumption *without* predator reproduction occurs with probability λ' . As we shall have the predator-prey interaction probability Λ depend on predator dispersal lengths (see below), it is convenient to introduce the following relations:

$$\lambda = \widehat{\Lambda}\widehat{\lambda}, \quad \lambda' = \widehat{\Lambda}(1 - \widehat{\lambda}), \quad \Lambda = 1 - \widehat{\Lambda}, \quad (5.2)$$

where $\widehat{\Lambda}, \widehat{\lambda} \in [0, 1]$ the conditional probabilities of the corresponding state transitions in our Monte Carlo implementation. More specifically, $\widehat{\lambda}$ is the predator reproduction probability given that it interacts with prey and predator-prey interaction occurs with probability $\widehat{\Lambda}$. For example, consider

$\widehat{\Lambda} = 1$, thus $\lambda = \widehat{\lambda}$ and hence $\lambda' = 1 - \widehat{\lambda} = 1 - \lambda$, i.e. $\widehat{\lambda}$ corresponds to prey consumption with predator reproduction and $1 - \widehat{\lambda}$ to consumption without reproduction. In contrast, when predators never interact with prey for $\widehat{\Lambda} = 0$, there is no reproduction nor consumption, and we find $\lambda = \lambda' = 0$.

Importantly, our SLLVM differs with existing studies using similar methods (e.g., [34, 44]), as our scheme contains a null-interaction wherein prey consumption does not necessarily lead to predator reproduction. Additionally, our model contains an explicit spatio-temporal coupling by having predators perform Lévy walks (see below). Critically, both these differences arise from our empirical observations that truncation effects (see below) resulted in non-Lévy predator dispersal. As such, the null-interaction ensures that predator dispersal in our model displays similar characteristics as optimal forager movement in sparse resource landscapes.

5.2.3 Predator dispersal

Predator dispersal on the lattice follows a Lévy walk with parameter α . In Lévy walks, foraging predators sample dispersal lengths, from a discrete inverse discrete power law [34, 46]

$$p(\ell) = \ell^{-\alpha} / \zeta(\alpha), \quad (5.3)$$

where $\zeta(\alpha) = \sum_{l=1}^{\infty} l^{-\alpha}$ the Hurwitz- ζ function that acts as the normalization constant. Recall from previous chapters that for $\alpha \leq 1$, the probability distribution function cannot be normalized. Different types of dispersal are characterized by different values of $\alpha > 1$ [20]. For $\alpha \geq 3$, predators diffuse normally (Brownian motion), whereas $\alpha \rightarrow 1$ results in ballistic (straight line) motion as dispersal lengths diverge. For intermediate values $1 < \alpha < 3$ predators exhibit superdiffusive (Lévy) behavior. Upon sampling a dispersal length (see Appendix 5.B), one of the cardinal directions (up, down, left, right) is randomly sampled, and the predator follows along this direction with steps of unit length (nearest neighbor hopping corresponding to fixed-velocity dispersal) until it either has traversed the sampled distance or the displacement is truncated. The latter can occur upon predator death, prey encounter, and predator encounter due to forbidden double occupation. For a more detailed description on the sampling procedure of dispersal lengths, please see Appendix 5.B.

5.3 Results

We simulate the predator-prey model on a square $L \times L$ lattice with $L = 512$ and prey habitat density $\rho = 0.2$. We distribute predators randomly on the matrix and prey individuals fully occupy habitat patches. Note that our results do not depend on the specific initial conditions. Measurements are taken when the system has converged to a quasi-stationary stable state after $T = 10^4$ Monte Carlo time steps (see Fig. 5.2). Unless mentioned otherwise, our results are reported as averages over 250 seeds.

Parameter	Symbol	Value
System lateral length	L	512
Monte Carlo time steps	T	10^4
Hurst exponent (spatial correlation)	H	$(0, 1)$
Prey habitat amount	ρ	0.2
Predator death probability	μ	$1/L$
Predator-prey interaction probability	$\hat{\Lambda}$	$1/\ell$
Predator reproduction probability	$\hat{\lambda}$	0.1
Prey reproduction probability	σ	0.1
Predator Lévy parameter	α	$[1, 3]$
Predator displacement length	ℓ	$p(\ell) \propto \ell^{-\alpha}$

Table T.5.1: Overview of model parameterization

5.3.1 Ecosystem fragility and choice of demographic rates

First, we motivate the choices of specific values of the demographic rates as to reflect systems of interest. As we let predator follow Lévy walks, the probability of predator death μ should be such that dispersal ranges are not exponentially truncated due to predator death. As such, in order to maintain characteristic length scales wherever Lévy walks optimize foraging behavior, we let $\mu = 1/L$. This effectively ensures that dispersal lengths can be sufficiently long, but do not often exceed environment sizes (cf. [47]), as we deem such behavior unnatural.

Next, we choose predator and prey reproduction rates such that systems with little fragmentation ($H \rightarrow 1$) are most fragile. Here, fragile systems are those wherein markedly different predator dispersal rates result in the system converging to an extinction fixed point. These occur due to prey extinction followed by predator extinction through overconsumption (nearest neighbor random walks for $\alpha \rightarrow \infty$) or through predator extinction due to underconsumption (ballistic motion for $\alpha \rightarrow 1$) [34]. Results indicate that, regardless of the prey reproduction probability σ , systems are most fragile for the conditional predator reproduction probability $\hat{\lambda} = 0.1$ (Fig. 5.1). It should be noted that rates within these regions represent ecologically relevant predators that are long-lived, slowly reproducing and highly motile. For the prey reproduction rate we choose $\sigma = 0.1$.

For predator-prey encounters, we consider that, when predators cross a site occupied by prey, the probability that they interact $\hat{\Lambda}$ decays with the current dispersal length, i.e. $\hat{\Lambda} = 1/\ell$, where ℓ the current length as sampled from Eq. (5.3). This assumption models intermittent search behavior, in which foragers interchange phases of non-reactive long, straight line displacements with reactive phases featuring shorter displacements and more frequent turns (see Section 1.3.1.3, Chapter 3 and, e.g., [48, 49]).

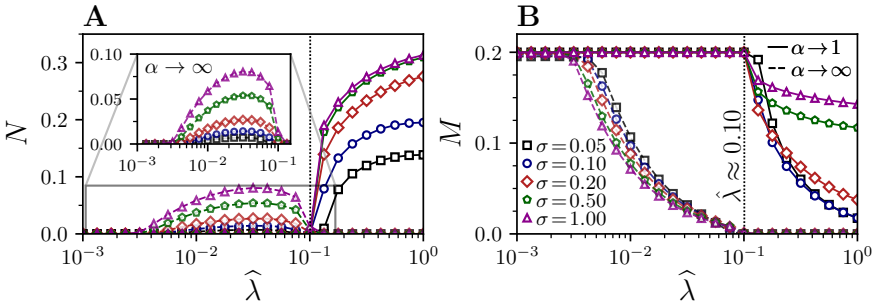


Figure 5.1: Influence of prey reproduction rate σ on population densities in the quasi-stationary stable state versus the predator reproduction probability $\hat{\lambda}$. Predator reproduction rate is given by $\lambda = \hat{\Lambda}\hat{\lambda}$ with predator-prey interaction probability $\hat{\Lambda} = 1/\ell$ and predator mortality rate $\mu = 1/L$. To determine demographic rates for which the landscape is most fragile, we compare ballistic predators (solid lines, $\alpha \rightarrow 1$, $\Lambda \rightarrow 1$) with predators that do nearest neighbor random walks (dashed lines, $\alpha \rightarrow \infty$, $\Lambda = 0$). Environments are generated with $\rho = 0.2$ and little to no fragmentation with $H \rightarrow 1$ (see Fig. 5.1). (A) Predator density N . Inset displays more detailed predator densities for predators with $\alpha \rightarrow \infty$. (B) Prey density M . Vertical dotted lines in (A) and (B) at $\lambda \approx 0.10$ indicate the predator reproduction rate for which the ecosystem is most fragile as markedly different movement strategies bring the system (close to) an extinction fixed point (see text).

An overview of the used parameters and their specific values is presented in Table T.5.1 and typical population dynamics of our model are shown in Fig. 5.2. Next, we study how predator foraging strategies, represented by the Lévy exponent α and habitat spatial structure, defined by the Hurst exponent H , impact population dynamics and result in patterns of irreversible habitat loss.

5.3.2 Population densities and species richness

Recall that we measure population sizes in the quasi-stationary stable state. Since prey reproduction rate is fixed in our simulations, equilibrium population sizes are determined by predator-prey encounter and predator reproduction rates. The long-time prey population size decreases monotonically as predators move from ballistic to Brownian foraging (Fig. 5.3). Predator density, however, is maximal for an intermediate value of the Lévy exponent for which its optimal value depends on the degree of fragmentation. For each degree of fragmentation H we distinguish three different regimes in population dynamics that result in different outcomes for the predator-prey interaction (Fig. 5.2).

First, due to our choice for the predator-prey interaction probability, ballistic predators ($\alpha \rightarrow 1$) rarely consume prey and thus go extinct. Upon predator extinction, prey proliferate until they reach their maximum popu-

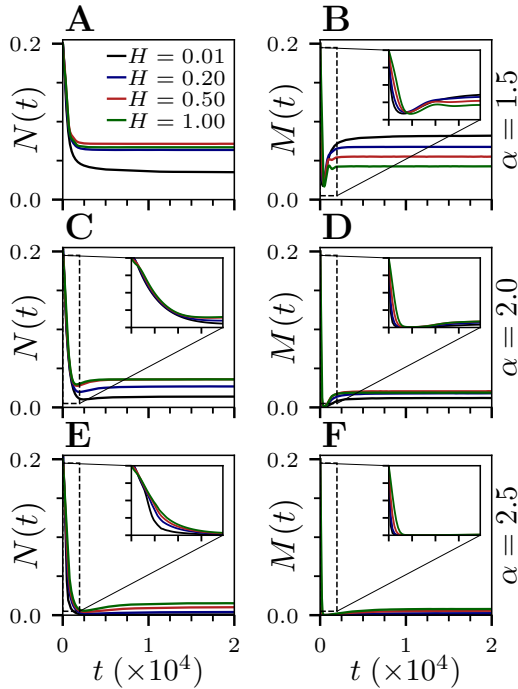


Figure 5.2: Time evolution of population densities for several Lévy parameters α and Hurst exponents H . The number of Monte Carlo time steps is $T = 2 \cdot 10^4$. Insets show early time dynamics up to $t = 2 \cdot 10^3$ Monte Carlo time steps. Note how quasi-stationary stable states are attained for $t \sim 10^4$. In general, stable population densities are lower than the initial densities.

lation size. Notice, however, that this population size does not correspond with prey habitat density ρ in fragmented landscapes because small habitat patches become irreversibly uninhabited (see below). Second, in the Brownian limit, $\alpha \rightarrow 3$, predation is intense and prey are overexploited regardless of the level of landscape fragmentation. This results in prey extinction followed by predator extinction due to lack of prey (Fig. 5.2). Note that predator extinctions are asymptotic due to our choice of the predator death rate and we still observe few individuals in our simulations when they are stopped. Third, for intermediate values of the Lévy exponent, our model predicts stable species coexistence at different population sizes that are jointly determined by predator movement, α , and habitat fragmentation, H .

For landscapes that display little fragmentation ($H \rightarrow 1$), habitat patches are large and predator relocations intersect with prey often. As a result, predation still occurs during the non-reactive phases represented by long displacements and predators maximize population densities with

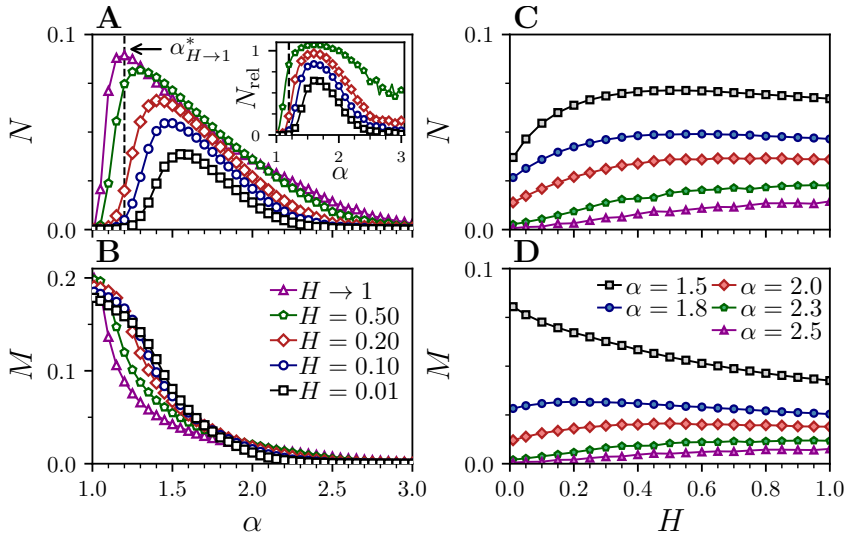


Figure 5.3: Effect of the Lévy parameter α and Hurst exponent H on population densities. Note that, for $\alpha \rightarrow 1$, we have $N \rightarrow 0$ as prey encounter rates fall since $\hat{\Lambda} = 1/\ell \rightarrow 0$. Additionally, for $\alpha \gtrsim 3$, we have $M \rightarrow 0$ due to overconsumption. As a result, these values of α are not shown. Other rate parameters are $\mu = 1/L$, $\sigma = 0.1$ and $\hat{\lambda} = 0.1$. (A) Predator density N as a function of α for different H . Dashed vertical line shows optimal Lévy parameter $\alpha_{H \rightarrow 1}^* \approx 1.2$ for $H \rightarrow 1$ and indicates predator extinction if predators cannot rapidly adapt to significant increases in fragmentation. (inset) Relative predator densities $N_{\text{rel}} = N_H / N_{H \rightarrow 1}$ displays decreases in N when predators forage with the same α in landscapes with higher fragmentation. Note that for some ranges of α there exists a preferred intermediate spatial correlation H (see text). (B) Prey density M as a function of α for different H . Prey density declines as predators are less dispersive for higher α . (C) Predator density as a function of H for different α . For sufficiently high dispersal rates (low α), we observe maximized predator densities for intermediate fragmentation. (D) Prey density as a function of α for different H . Note that for sufficiently high dispersal rates (low α) prey densities are highest in highly fragmented landscapes with $H \rightarrow 0$ (see text).

near ballistic foraging for $\alpha \approx 1.2$. In contrast, for highly fragmented landscapes ($H = 0.01$), the model tradeoff between displacement length and prey detection probability becomes more important because predator-prey encounters are more rare. It is thus more critical that predators adopt strategies that increase predation rates while ensuring sufficient encounters with prey. Balance is attained when short displacements are frequently interspersed with long-range relocations, leading to maximum predator population sizes for $\alpha \approx 1.6$.

Our results furthermore show that the range of foraging strategies that ensures predator survival becomes more narrow as habitat fragmentation

increases (inset Fig. 5.3A). This result suggests a stronger selective pressure on the foraging strategy in highly fragmented landscapes or potential extinction of predator species due to increased fragmentation if they are unable to rapidly adapt.

Interestingly, in the intermediate α regime, our model suggests that habitat fragmentation does not necessarily negatively affect population densities. Predator populations with $\alpha < 2$ display maximal densities for intermediate values of H (Fig. 5.3), although it should be noted that densities do not significantly decrease when fragmentation effects are less pronounced. Prey populations can benefit from high levels of fragmentation when predators are dispersive, approximately for $\alpha \leq 2$ (Fig. 5.3D). This benefit results from highly diffusive predators displaying low prey interaction rates and, as such, prey can avoid predation by taking advantage of fragmentation and spreading thinly. However, it is critical to note that for this to occur prey needs to initially inhabit these fragments. Moreover, they become more prone to demographic fluctuations (e.g., localized extinction) that can occur (see Section 5.3.3).

Next, we determine ecosystem health using a weighted species richness \mathcal{R} that captures how numerous predator and prey are relative to each other as well as the total population size within the environment. We define the species richness as

$$\mathcal{R} = ({}^1D - 1)(N + M), \quad (5.4)$$

where $1 \leq {}^1D \leq S$ the entropy-based diversity index with $S = 2$ being the total number of species in the system (see, e.g., [50] and Appendix 5.C for more details). Species richness mainly follows predator density. However, due to the effect of prey density, the predator foraging strategy α that maximizes species richness is consistently more ballistic than that maximizing predator density $\alpha_{\mathcal{R}}^* < \alpha_N^*$ (inset Fig. 5.6).

5.3.3 Fragmentation induces irreversible habitat loss

As mentioned above, predators may induce irreversible prey habitat loss in (highly) fragmented landscapes. Due to demographic fluctuations, prey goes extinct in patches that are not recolonized, as they are sessile. As a result, following predator extinction, prey population density does not converge to habitat density ρ (Fig. 5.3A). To investigate this further, we compute the patch depletion probability P_d as a function of patch size x by checking if the unique, separated patches (fragments) on the lattice contain prey at the end of our simulations. If they do not contain prey, we consider them depleted, which, in conjunction with their size (the number of sites) is registered.

Our results indicate that small patches have a higher probability of becoming depleted regardless of the predator foraging strategy α (Fig. 5.4), because they host smaller prey populations and are thus more sensitive

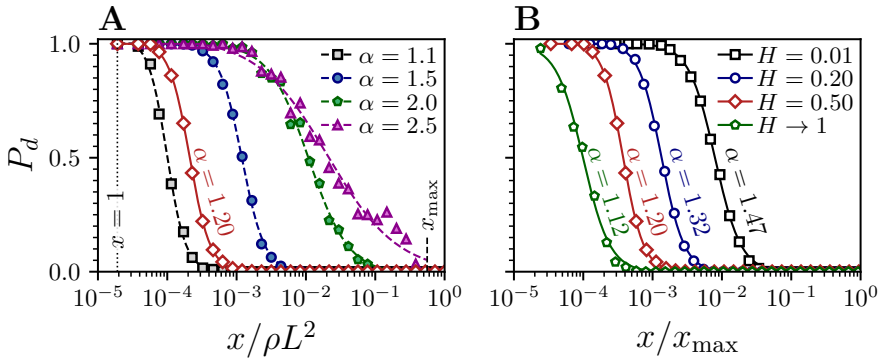


Figure 5.4: Influence of α and H on the probability of patch depletion, P_d , as a function of patch size x . All other parameters are as in Fig. 5.3. Solid lines are a guide to the eye. (A) The effect of α on patch depletion for intermediate fragmentation with $H = 0.5$. Dotted vertical lines indicate minimum patch sizes at $x = 1$ (single site). Dashed vertical line indicates maximum patch size for this particular level of fragmentation and patches with $x > x_{\max}$ do not exist, hence $P_d(x > x_{\max}) = 0$. Red curve displays P_d for the optimal response to maximize species richness for comparison ($\alpha = 1.2$, see inset Fig. 5.6). Note that less diffusive foraging strategies (small α) result in less depletion as ρ_{eff} remains high. (B) Patch depletion when predators respond optimally as to maximize species richness (i.e. $\alpha = \alpha_{\mathcal{R}}^*$), for different levels of fragmentation H . Specific values for α are indicated and have been extracted from Fig. 5.6. Note the normalization by x_{\max} as landscapes with low H contain patches of smaller sizes (Fig. 5.1, Appendix 5.A).

to demographic fluctuations. The effect of α on the depletion probability is stronger for intermediate patch sizes as higher values of α lead to more local predation and, as a consequence, higher patch depletion probability (Fig. 5.4). Importantly, significant patch depletion occurs even when predators adopt foraging strategies that maximize species richness (Fig. 5.4).

To evaluate the impact of patch depletion on habitat loss, we define the effective habitat density ρ_{eff} as the fraction of initial habitat ρ that potentially remains available to prey in the quasi-stationary stable state (Fig. 5.5). Ballistic foragers result in low levels of habitat loss, because predators rapidly go extinct and only few small patches are depleted (Fig. 5.4 and see also Fig. 5.3B). When α increases and short predator displacements become more frequent, depletion probability is higher for a broader range of patch sizes (compare, for example, curves for $\alpha = 1.1$ and $\alpha = 1.5$ in Fig. 5.4). As a result, effective habitat density is a monotonically decreasing function of the Lévy exponent and Brownian foragers minimize the effective habitat density regardless of the level of fragmentation (Fig. 5.5). However, in already fragmented landscapes, how much habitat is lost will depend on the level of fragmentation. Brownian foragers in slightly frag-

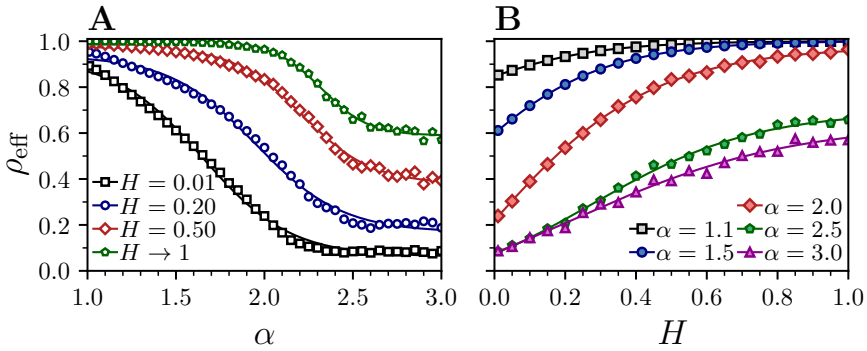


Figure 5.5: Influence of α and H on the effective habitat density ρ_{eff} . All other parameters are as in Fig. 5.3. Solid lines are a guide to the eye. (A) ρ_{eff} as a function of the Lévy parameter α for different H . Landscapes with higher fragmentation (low H) suffer greater losses of habitat. (B) ρ_{eff} as a function of the Hurst exponent H for different α .

mented landscapes ($H \rightarrow 1$) eliminate approximately 25% of the initial habitat. In highly fragmented habitats, this percentage is approximately 90% and most of the prey-predator dynamics occurs in the few, relatively large patches (but see Fig. 5.1B) that remain available for prey.

Next, we measure how habitat fragmentation affects effective habitat loss for different foraging strategies, α . As expected, ballistic predators minimize effective habitat loss because they minimize predation rates. In contrast, Brownian predators maximize effective habitat loss because they overexploit prey patches locally. Intermediate values of α maximize the difference between effective habitat loss at low and high fragmentation (Fig. 5.5B). For foraging strategies that maximize species richness and predator densities, increased fragmentation may result in an effective habitat loss of 40%. Importantly effective habitat loss is a nonlinear function of the fragmentation level with much faster decay when landscapes transition from slightly to highly fragmented (Fig. 5.6). Population sizes, however, decay much slower in response to increased fragmentation, illustrating the importance of foraging strategies in maintaining the stability of ecological communities in response to increased fragmentation and habitat loss.

5.3.4 Predator dispersal can reduce habitat loss

Finally, we emphasize on the stabilizing effects of dispersal by noting that habitat loss mainly results from small patches becoming irreversibly depleted, while only large patches remain inhabitable (Fig. 5.4). Therefore, effective fragmentation decreases (increased H) as spatial correlation on the fragments increases. Assuming predators can rapidly respond to such a change in fragmentation, our results indicate that α should decrease as

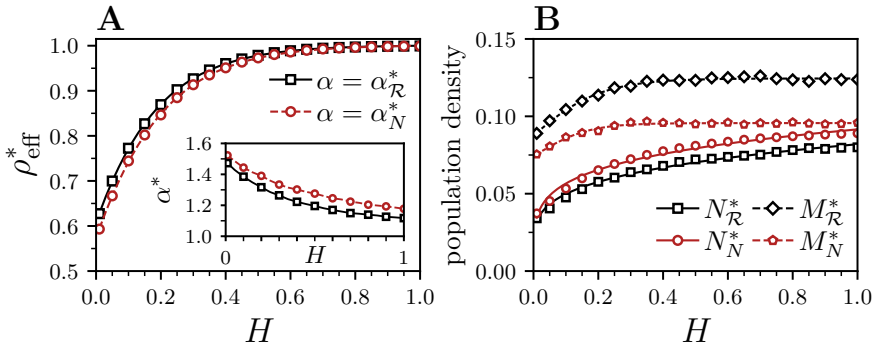


Figure 5.6: Effect of optimal predator response α^* to a particular level of fragmentation H . Optimal responses are either considered to optimize predator populations N or species richness \mathcal{R} , denoted by their respective subscripts. All other parameters are as in Fig. 5.3. Solid lines are a guide to the eye. (A) Effective habitat density ρ_{eff}^* . (inset) Specific optimal response α^* . (B) Predator and prey densities N and M . Loss of effective habitat results in decreases in population densities. Furthermore note that optimal responses result in decreased dispersal rates as fragmentation increases (inset), but that populations densities decrease regardless.

to maintain maximal population sizes (inset Fig. 5.6A). As a result, further habitat loss is inhibited, as habitat loss is less severe when α decreases (Fig. 5.5). Hence, our results conform to previous work that indicated that predator dispersal can stabilize irreversible habitat loss and population declines [34, 51–54].

5.4 Discussion

We have introduced a stochastic predator-prey model that allowed us to examine how fragmentation *per se*, foraging behavior and demographic rates influence population dynamics. Our model reveals that foraging behavior, as mediated by different dispersal strategies, and fragmentation jointly influence the stability of populations. We found that predator and prey populations, and the resulting species richness, are maximal for a specific dispersal strategy α that strongly depends on the level of habitat fragmentation H . Species richness was, however, maximized for consistently smaller values of α than predator densities, as lower values of α resulted in overall larger prey populations due to long-range dispersal reducing predation rates. Our results further indicated that increased fragmentation reduced the range of possible α -values that result in stable coexistence fixed points, suggesting a stronger evolutionary pressure on foraging strategies in highly fragmented environments. Moreover, optimal dispersal rates in landscapes with little fragmentation could result in predator extinction if fragmentation effects become significantly more severe if predators could

not rapidly adapt. Furthermore, as fragmentation increases, the effective habitat decreases regardless of the choice of α , resulting in spatially separated metapopulations that are more sensitive to local demographic fluctuations. This increased sensitivity results in irreversible habitat loss, even when predators respond optimally as to maximize species richness. However, our results indicate that predator dispersal can reduce, but not prevent, loss of habitat by adopting optimal demographic foraging rates.

In general, possible predator adaptations that resulted in the reduction of the amount of lost habitat were those that lead to increased dispersal rates. However, whereas such high dispersal rates might provide ecosystem stability, some species, such as small mammals [55] and amphibians [56], are instead characterized by their low dispersal abilities. Within the context of our model, these species effectively represent predators with high α , for which our results indicate major extinction events and habitat loss when environments become increasingly fragmented. Therefore, within highly fragmented landscapes, species with limited dispersal possibly induce severe population instability within their niche and, subsequently, in their entire trophic network [57]. It is therefore of critical importance to assess species-specific dispersal rates and how it affects their specific habitat in future models [58].

In this work, we did not consider possible responses that prey populations could display to counteract decreases in (local) populations. Within the context of our model, the only possible response by prey to prevent local extinction events is to greatly increase their reproduction rate. Therefore, our results suggest that evolutionary pressure in fragmented landscapes favors fast-reproducing species if they are unable to travel to distant fragments. In natural systems, however, prey is often not sessile but can instead disperse and thereby respond to increased predator densities [59]. Additionally, it has been suggested that refuges, i.e. areas where prey can avoid predation, increase population stability (see, e.g., [60, 61]). As prey dispersal and refuge stability depends critically on the spatial structure of prey habitat, further investigation into predator-prey responses to increased fragmentation is much needed.

To the best of our knowledge, we are the first to present a spatially explicitly stochastic predator-prey model wherein predators are assumed to exhibit optimal foraging behavior. Our investigation as to how landscape structure, foraging behavior and demographic rates determine population stability, cements the critical role of foraging patterns on population stability and provides motivation for including spatially explicitly and individual-based movement into population future models.

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Appendices

5.A Fragmentation and patch sizes

Here, we discuss the effects that fragmentation *per se* (hereafter; fragmentation) has on the habitat distribution. Notably, fragmentation effects are weaker when habitat density is high (as apparent in Fig. 5.A.1, left). This is exemplified by noting that increased fragmentation decreases average patch sizes, as smaller patches become more frequent as H decreases, while large patches become (near) nonexistent (Fig. 5.A.1, right). We consider landscape connectivity to be defined by percolation as the probability p of fragments connecting to either side of the lattice. For large ρ we find $p \rightarrow 1$ regardless of the value of H (Fig. 5.1) and as such, the largest patches contain most of the available habitat, effectively reducing our predator-prey model to one without habitat restrictions for prey (i.e. a homogeneous landscape, as in, e.g., [44, 45]).

5.B Sampling of Lévy walks on a lattice

As our lattice corresponds to discrete spatial locations for both prey and predators, predators sample flight lengths from a discrete inverse power law. Clauset et al. [46] provides sampling methods for discrete, power law distributed variables. However, when the Lévy parameter indicates ballistic motion for $\alpha \rightarrow 1$, practical implementations of their methods might fail due to integer overflows as flight lengths grow increasingly large. To circumvent this, we instead sample from a truncated power law [62], where

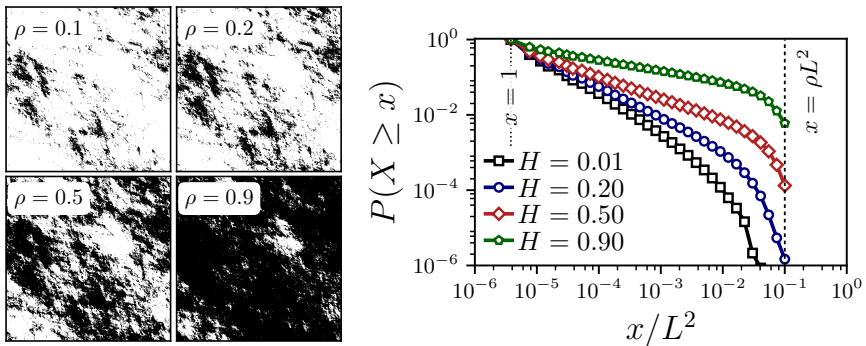


Figure 5.A.1: (left) Fragmented landscapes of different prey habitat densities ρ for a fixed spatial correlation $H = 0.1$. The effect of fragmentation reduces as ρ increases (see text and Fig. 5.1). (right) Influence of H on distribution of patch sizes x for $\rho = 0.2$. $P(X \geq x)$ is the complementary cumulative distribution function of patch sizes being equal or larger than x . Results are obtained for 512×512 landscapes. Vertical dashed (dotted) line indicates maximum (minimum) possible patch size.

our lower truncation is $\ell_{\min} = 1$, the unit lattice spacing. For choosing the upper truncation, one has to take care to ensure long flights are those wherein predator-prey interactions are rare, i.e. $\hat{\Lambda} = 1/\ell$, cf. intermittent random searches (for an overview see [49]). To this end, we choose ℓ_{\max} such that the probability of a predator that is executing ballistic motion with $\alpha \rightarrow 1$ is, in practice, negligible. As we take averages over a number of experiments in the order 10^2 – 10^3 , we choose ℓ_{\max} such that the probability of detecting prey when $\alpha \rightarrow 1$ is smaller than 10^{-3} . As the predator-prey interaction probability is a Bernoulli trial with the average number of prey encounters for a ballistic predator equal to ρL , we can conclude that $\ell_{\max} \sim 10^5$ leads to the desired result. Note that in this regime, as we choose $\mu = 1/L$, it becomes unlikely that predator flight lengths reach ℓ_{\max} , as both the probability to survive for this long is very small and our number of Monte Carlo steps is not sufficient as $T = 10^4$. As a result, ballistic foragers, in practice, do not interact with prey for $\ell_{\max} \sim 10^5$, as desired by having $\Lambda = 1/\ell$ (see Fig. 5.3). More specifically, we choose $\ell_{\max} = 200L = 102400$ in all of our experiments, with $L = 512$.

As for the sampling procedure, we define the complementary cumulative distribution $P(\ell)$ as the probability of a sampled length \mathcal{L} to be larger or equal to ℓ , i.e.

$$P(\ell) = \Pr(\mathcal{L} \geq \ell) = \sum_{y=\ell+1}^{\ell_{\max}} p(y), \quad (5.5)$$

where

$$p(y) = y^{-\alpha} / (\zeta(\alpha, \ell_{\min}) - \zeta(\alpha, \ell_{\max})), \quad (5.6)$$

with ℓ is the flight length of predator dispersal and $\zeta(\alpha, l) = \sum_{n=0}^{\infty} (n+l)^{-\alpha}$ the Hurwitz- ζ function. To sample predator displacement lengths, we draw a random number r and compute ℓ that satisfies $P(\ell) = 1 - r$. As $P(\ell)$ cannot be inverted in closed form, we execute a binary search within the interval $[\ell_{\min}, \ell_{\max}]$ to solve for ℓ [46, 62]. Because we are interested in discrete samples, we continue the binary search until the value of ℓ is narrowed down to $k \leq \ell < k + 1$, for some integer k . Then, we discard the non-integer part of ℓ to be used as the discrete sample. Binary search is implemented in many standard libraries, and can be efficiently performed as to draw many sampled efficiently. Even so, one profits from pre-computing the Hurwitz- ζ functions for all values $\ell \in [\ell_{\min}, \ell_{\max}]$ since computation of these values can be computationally expensive.

5.C Species richness and ecosystem health

While population densities are of relevance to determine ecosystem health, it can be worthwhile to additionally discuss ecosystem ‘health’. In ecology, diversity indices are often used to indicate ecosystem health, where

primers such as biodiversity (i.e., the number of species) are often of interest. Additionally, *species richness* can measure the number of species relative to the total number of individuals. In this work, we consider the effective species diversity, Hill number, or ‘true diversity’, qD , to capture ecosystem health (see e.g., [50]). The effective species diversity is an entropy-based measure and defined as

$${}^qD = \left(\sum_{s=1}^S p_s^q \right)^{1/(1-q)}, \quad (5.7)$$

where S is the total number of species, and p_s the probability of sampling species s when random sampling from the total population of all individuals, i.e. the proportional abundance of species s . q defines the sensitivity of the true diversity, where $q > 1$ weights the more abundant species more heavily and $q < 1$ weights given to rare species are exaggerated. For $q = 1$, weights for all species are equal and the true diversity can be defined by using the well-defined the limit

$${}^1D = \exp \left[- \sum_{s=1}^S p_s \ln p_s \right]. \quad (5.8)$$

However, the diversity index with $q = 1$ does not take into account the total population size and is effectively biased towards systems with equal species numbers. For example, a two-species systems, as the predator-prey system studied here with numbers N and M , is equally ‘diverse’ for $N = M = 1$ as for $N' = M' = 100$, while we argue here that the second system is more ‘healthy’ as it contains more organisms. To account for this bias, we define the species richness as \mathcal{R} as

$$\mathcal{R} = ({}^1D - 1) \cdot \sum_{s=1}^S N_s, \quad (5.9)$$

where N_s the spatially averaged density of species s per unit area. We subtract 1 from the true diversity to bring its value between 0 and 1. $\mathcal{R} = 0$ conforms to systems where there is only one species remaining or when there are no organisms within the system, whereas $\mathcal{R} = 1$ corresponds to a fully occupied system with equal abundance of all its species.

For our particular system, we plot the species richness \mathcal{R} in Fig. 5.C.1. Clearly, species richness predominantly follows the characteristics of predator populations (Fig. 5.3), however the optimal predator responses are consistently smaller due to the influence of prey population. In effect, when α decreases, prey populations increase as predator-prey interaction rates fall (Fig. 5.3). Therefore, species richness increases as α (slightly) decreases, as those systems support more prey.

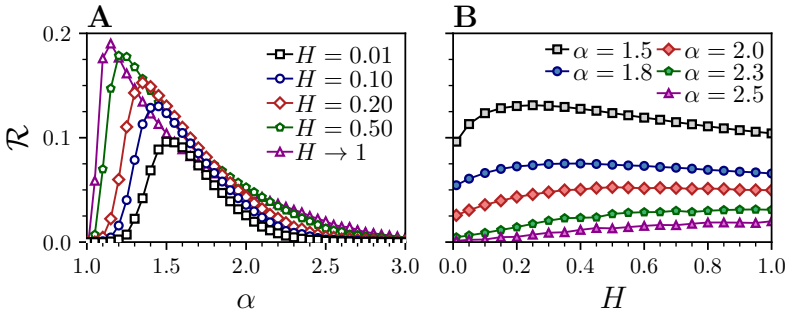


Figure 5.C.1: Influence of α and H on the species richness \mathcal{R} . Note that \mathcal{R} mainly follows predator density (Fig. 5.3) but effects of prey density results in consistently more ballistic dispersal to maximize \mathcal{R} when compared to predator density (inset Fig. 5.6). All other parameters are as in Fig. 5.3.

We would like to emphasize here that other definitions of species richness exist and that its definition should depend strongly on the context wherein it is applied (cf. Gorelick [63]). For our intended purposes, i.e. a two species predator-prey model, the definitions of Eqs. (5.8) and (5.9) serve as a simple indicator of the biodiversity – thus ecosystem health – in our systems. We did not observe qualitative changes in maxima (i.e., optimal responses) to different entropy-based measures.

6

Conclusion and outlook

This dissertation has discussed optimal foraging and its dependence on various factors such as individual complexity, interactions with other foragers and environmental conditions. More specifically, we addressed four main research questions which we shall revisit and critically review below.

Research question 1. *How can an individual forager benefit from spatial memory when resources are distributed within patches?*

In Chapter 2, we discussed a single forager that employed spatial memory to learn a distribution over patch locations to improve foraging efficiencies. We introduced a hybrid foraging strategy, wherein random searches following a Lévy walk were interchanged with informed relocations by sampling goal states from the learned memory. We presented spatial memory as an ensemble of Gaussian mixture models (GMMs), as (i) GMMs are universal function approximators, thus able to learn, in principle, any (spatial) distribution; (ii) GMMs can be learned incrementally, thereby making it possible for the forager to adapt its memory based on novel experiences; and (iii) an ensemble of GMMs provides a measure of uncertainty that allowed the forager to make decision based on the estimated correctness of the learned spatial distribution. We presented a system wherein the random search could be truncated when the forager had not encountered resources in some time. The longer the forager traveled without resource encounter, and the lower the uncertainty of the learned distribution, the more likely the forager was to stop exploring, by random search, in favor of exploiting, by informed movement. Using this hybrid foraging strategy, we studied how the rate of memory exploitation influenced the foraging efficiency.

As we considered the foraging efficiency depending on the inverse of the traversed distance, our results indicated that non-destructive foraging was optimized when memory exploitation rates were high. This was the result from frequent revisitation of known patch locations, effectively penalizing exploration as it resulted in increases in travel distances. However, extensive memory exploitation restricted the forager to explore very little of the environment, thereby significantly reducing the diversity of visited patches. Most interestingly, we showed that this spatial restriction leads to a change in diffusive properties of the foraging task, suggesting that memory can significantly affect observed motion patterns in foraging species. Our results thus indicate that spatial memory introduces a trade-off between high foraging efficiency, through exploitation with low diffusion, and high patch diversity, through exploration with high diffusion; a trade-off, called the *exploration-exploitation* trade-off, that is not trivially solved.

Possible solutions that optimize this trade-off depend strongly on the characteristics of the resource distribution. Whereas we assumed non-destructive foraging, i.e. static resource distributions, many environments possess some dynamics, either through interactions (e.g. destructive foraging) or intrinsically (e.g. seasonal availability). Evidently, memory is not expected to be useful in rapidly changing environments [1]. However, memory might still be useful when resources regenerate over specific timescales known (or estimated) by the forager, effectively allowing foragers to revisit patches once these have recovered [2, 3]. Interestingly, consecutive relocations to known patches, i.e. deterministic displacements, have been shown to exhibit the scale-free characteristics typical for Lévy walks [4], suggesting that Lévy walks can result from interactions with the environment, similar to how our model influences the spatial characteristics of forager displacement. How exactly optimal foraging behavior is influenced by spatial characteristics and cognitive capabilities, and how the trade-off between exploration and exploitation can, under some circumstances, be solved, remains an open question that warrants further research.

Furthermore, we discussed environments with a single type of resource, yet our results might extend beyond this particular case. As many foraging animals rely on a diverse set of resources in order to survive [5, 6], e.g. food and water, our results highlighted that the type of foraging strategy should depend strongly on the current state and needs of the forager [7]. Despite our study into optimal foraging with memory lacking an internal state or preference, we believe that the ensemble of mixture models remains an excellent candidate for decision making during foraging. In particular, each component of the mixture can be weighted differently as to reflect patch contents, or separate components of the mixture can be established to represent different types of memory, such as short-term and long-term memory. Therefore, whereas we did not explore potential ef-

fects of state-dependent weightings, we believe that we have highlighted a potential spatial memory candidate, and have identified strengths and weaknesses of this approach.

Finally, we would like to mention that we did not discuss biological relevance of our particular choice for the spatial memory model. As spatial memory is critical to understand movement, and thus foraging behavior, of animals [8], we argue that more research into the specific type of spatial memory that foragers exhibit is needed in order to fully understand how foraging behavior and cognition interact.

Research question 2. *How does resource fractility determine the effectiveness of group foraging strategies on groups subjected to intraspecific competition?*

Many foragers are not solitary but forage in groups. We presented an agent-based model to quantitatively study the effect of the resource distribution on the effectiveness of simple group foraging strategies. We considered a group of foragers that exhibited intermittence in their random searches, by changing their foraging behavior on resource detection. More specifically, intensive searches were triggered when a resource was detected, as it indicated encounter of a patch rich in resources. This switch in behavior, from an extensive (global) to an intensive (local) search, signified high local resource densities and could be detected by nearby conspecifics that subsequently joined the forager in their successful foraging efforts. However, as foraging was destructive, increased forager densities on the patches lead to competition for the limited resources within the patch.

By controlling the degree of clustering ('patchiness') of the resource distribution, we quantitatively determined the benefits of joining, both at the individual and at the group level. At the group level, our results indicated that joining others was only advantageous if resources are sufficiently clustered and competition rates were low. Effectively, this indicates that group foraging is only beneficial when patches contain sufficient resources to facilitate a fair distribution of resource intake rates for all foragers on that patch. When patches contain little resources instead, or when group sizes (thus forager densities on the patches) grew, we showed that joining others is, in general, not a good strategy. In contrast, on the individual level, foragers might benefit from these large aggregations when their incentive differs from optimizing their average foraging efficiencies. We considered a particularly important alternative incentive: survival. By computing the variation in resource intake rates, we found parameter regions wherein group foraging resulted in lower foraging efficiencies, individual advantages were highest. Interestingly, our results conform with empirical observations that many foragers resort to so-called *low mean, low variance* strategies [9], instead of optimizing average (group level) foraging efficiencies.

Whereas an underlying assumption in OFT is that foragers, either individual foragers or group foragers, solely strive to optimize foraging efficiency [10], several arguments against this viewpoint have been discussed

in the literature [11, 12]. In our case, increased survival rates by reduced variation in resource intake is a prime example of other objectives that real-world foragers might pursue. Additionally, foragers might be subjected to predation themselves, and thus traveling and foraging in groups reduces individual predation risk [13–15]. In general, reasons to aggregate on patches or forage in groups can be plentiful, and should not be assumed to necessarily originate from OFT. It would therefore be of interest to extend our model to include more incentives for joining others, such as predation, or discuss foraging in, e.g., fixed-size groups [16].

Finally, we assumed individual foragers to possess relatively simple cognitive capabilities. As an example, we did not consider foragers to take into account forager densities when at the verge of joining, while these are known to influence decision making during group foraging [17]. Additionally, our model corresponds to a homogeneous system of foragers, wherein foragers do not possess a preference and therefore do not base their decisions on internal states such as hunger. However, realistic groups of foragers are often inhomogeneous instead [18, 19], and individual traits (e.g., preference to be a producer or scrounger, as discussed in Section 1.4.1) are important to include in future models on group foraging.

Research question 3. *How can altruistic behavior increase collective foraging efficiencies, and how does it depend on the patch persistence?*

In contrast to competitive systems, e.g., resulting from competition for limited resources, many systems instead display feats of altruism, bringing about collective behavior. To investigate how the effectiveness of altruistic behavior depends on the spatial distribution of resources, we introduced a system wherein foragers could actively recruit others towards patches instead of exploiting the patch by themselves. More specifically, we studied foragers that could estimate conspecific encounter rates and, using this estimation, foragers could decide whether to start recruiting others when detecting a patch. We focused on systems wherein resource density (patch quality) and patch duration were positively correlated. As a result, within our framework, foragers resorted to a threshold-based decision on patch detection. Only patches of sufficient duration provided enough time to recruit others, thereby triggering (active) recruitment behavior.

Our results indicated that active recruitment increased collective foraging efficiencies, but only when patches were difficult to locate (sparse) and sufficiently persistent. When patch durations were, on average, short, recruiting behavior was unlikely to lead to conspecific encounters and it would have been more beneficial if the recruiting forager exploited the patch by itself instead. Our results further supported this notion by showing that advantages of active recruitment depended strongly on effective forager densities. We compared active recruitment, by active search for conspecifics, with passive recruitment, by simple broadcasting of the patch

location, and showed that active recruitment is only beneficial when effective forager densities were low. When interactions with conspecifics were frequent, i.e. when forager numbers were high or when interaction radii were large, passive recruitment was more efficient. However, as many collective systems exhibit short interaction radii [20–22], our results indicated that collective systems benefit from active recruitment, provided patches were sufficiently persistent. Most interestingly, our results furthermore indicated that specific choice of the recruitment threshold was less important than the decision whether to recruit at all. This can have profound influences to applications in artificial systems, as it appears that intricate decisions and high cognitive capabilities are not necessary to gain benefits from recruitment behavior.

It should be noted that there do exist collective systems that can transfer information across potentially large distances, e.g. using sound [23–25]. Additionally, central nesting sites can be used for information transfer [26, 27]. As we considered ephemeral aggregations wherein only information on a single patch location was transferred, higher interaction complexity could potentially unveil more efficient foraging behavior. Additionally, we did not take into account more intricate collective decision making models that are observed across many taxa (see, e.g., [28–35]). Therefore, we believe that further study on how information is processed by a collective system is needed to elucidate advantages and disadvantages of collective foraging.

Research question 4. *How does landscape fragmentation influence populations of optimal foragers and how can optimal foraging responses lead to changes in spatial configurations affect the landscape?*

Finally, we addressed how foraging behavior translates to population dynamics and how it interacted with landscape structure. To this end, we transformed our forager-resource system, without population dynamics, to a predator-prey system, with population dynamics, assumed to be sessile and could only inhabit spatially separated patches, representing a fragmented landscape, while foragers could instead disperse and move in between the patches using a Lévy walk. Our results predicted that the effects of fragmentation *per se* on population densities were mostly negative, however effects depend strongly on forager dispersal rates. More specifically, landscapes that displayed little fragmentation resulted in optimal forager movement to be highly diffusive, as to both visit far away patches while not overexploiting them upon arrival. Increases in fragmentation were associated with decreases in optimal dispersal rates, as highly diffusive foragers were much more likely to miss potential prey encounters compared to less diffusive movement. Furthermore, we discussed species richness as a measure of ecosystem health, and showed that it predominantly followed forager densities and not prey densities. Most importantly, however, our results show irreversible habitat loss resulted from local predation and that

this decline in effective habitat was exacerbated in highly fragmented environments. As we considered prey to be sessile, highly fragmented systems contained numerous barriers between habitat patches that prey could not cross. Our results indicated that small patches were much more likely to become depleted and that subsequent habitat loss generally lead to reductions in population densities. However, most interestingly, we showed that optimal responses to decreases in available habitat could reduce, but not prevent, habitat loss, highlighting the importance of dispersal on the stability of ecosystems [36, 37].

Whereas our results appeared to indicate that fragmentation nearly always results in negative effects for population persistence and biodiversity, it should be noted that our model considered prey as sessile species. Evidently, for such species, barrier effects are larger than when prey is motile. As an example, if two patches within our model were separate by only a very small distance, prey could not move from one patch to the other. In more natural settings, prey might react to forager densities (i.e. avoidance, see e.g. [38, 39], or might itself forage using specific dispersal characteristics (i.e. multi-species systems, see e.g., [40]). Within our model, this can be realized both by letting prey disperse, e.g. by having prey disperse using a Lévy walk as well, or by allowing prey to inhabit sites in between the fragments by reducing the mortality rate induced by barriers. Especially the latter is of interest for conservation efforts, as the areas in between fragments greatly influence population persistence [41, 42].

Additionally, movement between separated fragments can be controlled by placement of so-called corridors [43]. This effectively increases the connectivity of fragmented landscapes, which is crucial to stability of many ecosystems across the globe [44]. To this end, it would be interesting to extend our model to include such an increased connectivity, as it might provide stabilizing effects by slowing down rates of habitat loss and thereby prevent significant decreases in population densities.

Finally, the results presented in this dissertation highlight that decisions underlying optimal foraging are incredibly complex and, as such, are likely to affect entire populations. In particular, demographic parameters, such as reproduction and mortality rates, are undoubtedly a function of, e.g., group size, resource availability and foraging strategy. Therefore, we argue that going forward, population models should integrate individual-based models, such as OFT, with population models (see, e.g., [45]).

Future perspectives

Obviously, this dissertation does not provide definitive answers to the posed research questions, nor was it intended to. Below, we shall present a general outlook on optimal foraging and identify future avenues that we argue are worthwhile of further study.

Optimal foraging behavior The value of understanding optimal foraging behavior is derived from its ubiquity: almost all organisms need to search in order to survive. While several significant contributions towards understanding this process have occurred in the last few decades, we are still far from knowing how optimal foraging behavior emerges. Interestingly, optimal foraging is of interest to scientists from vastly different backgrounds, as it integrates mathematical theories and physical properties of random walks with behavioral characteristics of (collective) decision making. Therefore, we argue that, going forward, understanding optimal foraging behavior will require an interdisciplinary approach.

Current advances on the study of optimal foraging, including the ones presented in this dissertation, often resort to identifying how and when specific foraging behavior is optimal. However, very little research has been done on elucidating the biological mechanisms that generate optimal foraging behavior [46] (but see [47]). As even simple organisms display complex, adaptive foraging strategies, we argue that researchers should now focus on developing explainable models for such model organisms as to gain a grasp on the mechanisms underlying optimal foraging behavior. Potentially, study of these mechanisms might uncover a universal framework that can explain how optimal foraging characteristics came to be.

Foraging from an evolutionary standpoint Whereas the work in this dissertation addresses optimal foraging strategies, it does not contain any discussion on how foraging success might result in evolutionary pressure towards evolving complexity. For example, it has been suggested that foraging benefits of spatial memory in predictable environments might have acted as a stimulus for improved cognition [48, 49]. Similarly, why many animals choose, or do not choose, to live in groups could also have originated from foraging arguments, and could perhaps have been an underlying factor in the history of human civilization [50]. Therefore, we argue that future studies into how observed foraging behavior can be shaped by an evolutionary pressure to forager efficiently will provide incredible amounts of insights on why animals forage as they do.

From a more practical standpoint, this means that evolutionary models, e.g. foraging systems with birth and death processes subjected to evolutionary pressure, and optimal foraging models should be integrated. Research into such systems might isolate what fitness function foragers optimize, how emerging optimal strategies depend on critical parameters such

as forager density and resource availability, and how these insights might explain the foraging behavior that is observed in natural systems.

Ecological consequences of optimal foraging Finally, we would like to address foraging from a more conservational viewpoint. As ecosystems all over the world are rapidly changing, most often due to anthropogenic influences, it becomes of utmost importance to understand how these changes affect the animals living within. To predict how animals will respond to these negative effects, such as habitat loss, we first need to know how their behavior depends on the environmental conditions. Whereas the work presented in Chapter 5 explores how landscape fragmentation might influence foraging behavior, much more work is needed to fully understand the influences of our own actions before it is too late. Additionally, it has recently become apparent that species experience intricate trophic interactions [51], indicating that effects on populations of many interacting species are incredibly difficult to predict [52, 53]. Therefore, we should now start to include these complex interactions into population models, and discuss the influence of rapid changes to ecosystem health and stability. In doing so, we might possibly discover potential solutions to suppress the current rate of biodiversity decline.

Final remarks

At the very least, we hope to have introduced some to optimal foraging theory as a means to find their lost items just a little quicker. Going forward, we argue that despite the fact that the open challenges regarding optimal foraging are difficult to address, the research contained in this dissertation contributes to this debate and hopefully assists some to continue studying foraging behavior, its origins and its future.

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