

# Group size and resource fractality drive multimodal search strategies: A quantitative analysis on group foraging

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## ABSTRACT

Foragers within a group might increase individual foraging efficiencies by using public information to assess local resource availability. This information is often expressed as a change in behavior at resource encounters, which can be detected by nearby individuals. When the resource landscape displays sufficient degrees of clustering or fractality, joining nearby conspecifics in their successful foraging efforts becomes an attractive strategy. However, when group sizes increase, joining others might become less effective due to increased levels of intraspecific competition. In this work, we introduce a trimodal Lévy search in fractal resource landscapes, where highly diffusive, extensive searches are interchanged with localized, intensive searches and informed searches guided by attraction to successful conspecifics. Using an agent-based model, we are able to quantitatively determine what environmental characteristics facilitate joining to be beneficial on both the group and the individual level. We find that joining others is advantageous on the group level, but only if resources are sufficiently clustered and group sizes and joining ranges are not too large. In contrast, individual advantages, expressed as an increased survival rate mediated by a reduced variation in resource intake rate, are largest precisely in parameter regions where group benefits were smallest. These results highlight both the reach of a relatively simple agent-based model based on multimodal random searches, and the notion that groups might not necessarily optimize foraging efficiency when more strict conditions, such as survival, need to be met.

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## 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 [1–3]. In addition, foragers within a group might benefit from interactions with others in order to further increase their foraging efficiency [4,5]. For example, detecting successful nearby conspecifics and joining them has been a well-documented phenomenon in natural systems [6–11]. However, when group sizes increase, intraspecific competition additionally increases [12–19], 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

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not only highly dependent on the resource distribution, but also on individual decision processes and interactions between foragers [20].

Traditionally, foragers joining successful others have been studied in the context of information sharing systems [21,22] or producer–scrounger systems [23,24]. 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 [25]. Such joining mechanisms can reduce variations in resource intakes as it equalizes the distribution of resources, possibly leading to higher group search efficiencies [11,26]. In the producer–scrounger framework [22,27], 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 [24,28], where field studies have identified intricate producer–scrounger dynamics within populations of baboons [29], rooks [30] and finches [31], 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 [32,33]. Most often, separate patches are the result of power laws that describe the underlying resource distributions [34,35], leading to scale-free, fractal resource landscapes [36–44]. Such resource distributions typically increase the benefits of joining, since resources themselves are more difficult to locate, but the patches contain high numbers of resources [45]. 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 [42,46], thus allowing for the description of random searches as Lévy walks or flights [2,47]. Whereas the robustness of these Lévy searches has been widely established [1,3,48–50], whether animals truly execute Lévy walks is currently still up for debate [51–56]. Nevertheless, increasing evidence shows existence of Lévy walk characteristics across a wide variety of organisms, ranging from micro-organisms such as bacteria [57], cancer cells [58] and T cells [59] to aquatic animals [60], and from insects such as honey-bees [61] to mammals such as deer [62,63] and even human hunter–gatherers [64]. Moreover, recent theoretical advances seem to point towards Lévy walks as random searches for optimal area coverage [65] and for optimizing the time needed to detect sparse targets of different sizes [66].

The characteristics of Lévy walks depend heavily on environmental influences [60], 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. [1] can be adapted to a multimodal (adaptive or composite) search [67,68]. 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 collective behavior such as aggregation [5,69].

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 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 level 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 favor strategies that result in small variation, as long as minimum energetic constraints are met.

We have organized the work as follows. First, we introduce the fractal resource landscape in Section 2, and discuss the bimodal and trimodal Lévy searches in Section 3, and Section 4 respectively. In Section 5 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 6 and present an outlook on the implications of our work.

## 2. 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 [5,70]. Characterizing 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 [49,55]. The distribution with Lévy parameter  $\gamma$  is defined as

$$p_\gamma(\ell) = \begin{cases} Z_\gamma \ell^{-\gamma} & \ell_0 < \ell \leq L \\ 0 & \text{otherwise,} \end{cases} \quad (1)$$

where  $Z_\gamma$  is the normalization constant and  $\ell_0$  and  $L$  are the minimum respectively the maximum distances. The orientation angle  $\theta$  between subsequent resource placements is sampled uniformly between 0 and  $2\pi$ . As such, the generated resource distribution represents a Lévy dust [71,72], where each point in the flight represents a resource location.

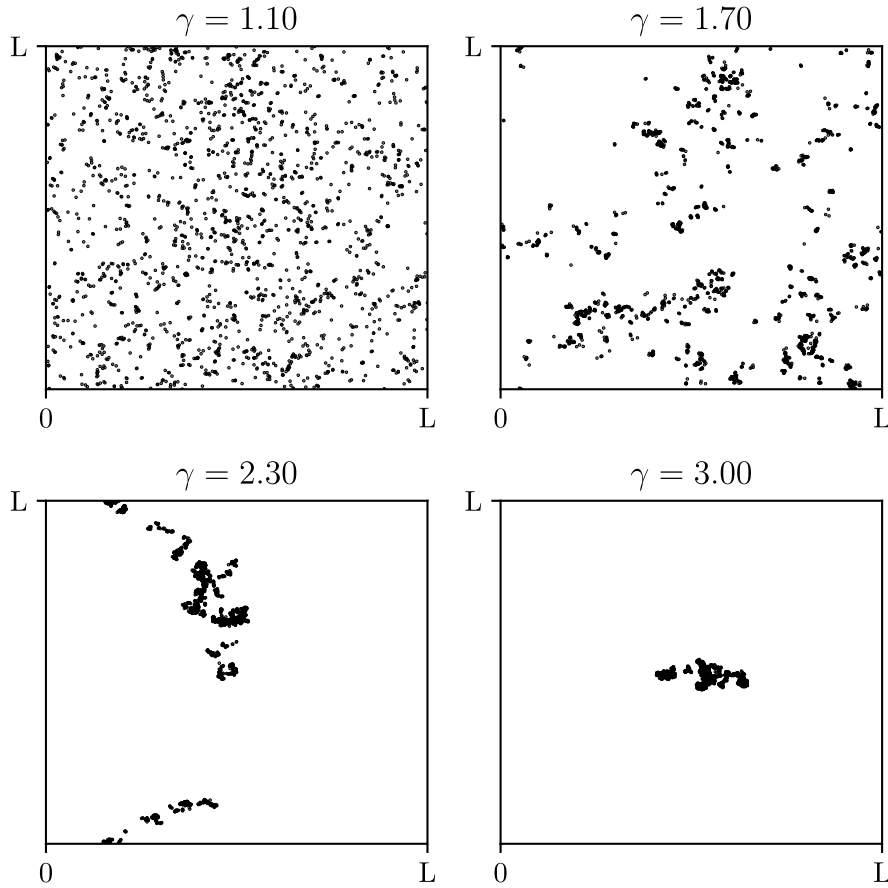
Lévy flights capture different resource distributions, related to the properties of the distribution (see Fig. 1). For  $\gamma \rightarrow 1$ , distances between subsequent resources are large, resulting in a (near) uniform distribution due to the periodic boundaries (see also [65]). When  $\gamma \geq 3$ , 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  $\gamma$  will asymptotically converge to the same distribution, being dense and uniform [49]. However, since realistic environments have a finite number of resources, the significant structural differences for different values of  $\gamma$  become apparent even for relatively large values of  $M$ , as seen in Fig. 1.

## 3. 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  $\alpha$  [68,73]. 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 [47,49]. Then, similar to Eq. (6), flight lengths are sampled from an inverse power law as

$$p_\alpha(\ell) = \begin{cases} Z_\alpha \ell^{-\alpha}, & \ell_0 < \ell \leq L \\ 0 & \text{otherwise,} \end{cases} \quad (2)$$

where  $Z_\alpha$  the normalization constant. Foragers walk along the sampled flight lengths with step size (fixed velocity)  $\ell_0$ , with the direction  $\phi$  sampled uniformly from 0 to  $2\pi$ . The parameter  $\alpha$  defines the spatial characteristics of the movement. Hence, Lévy walks encompass a wide range of different movement patterns (diffusion), ranging from ballistic motion for



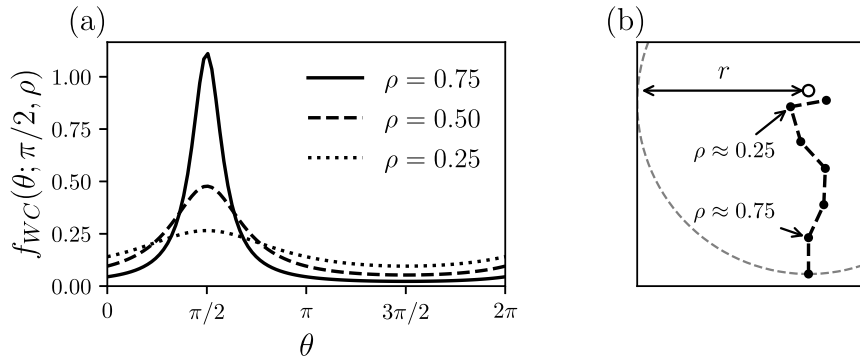
**Fig. 1.** Examples of typical resource distributions of  $M = 2048$  resources in the  $L \times L$  environment for different Lévy parameters  $\gamma$ . The periodic boundary effects are apparent when  $\gamma$  decreases, resulting in increasingly uniform distributions for  $\gamma \rightarrow 1$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

$\alpha \rightarrow 1$  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. (2) towards a Gaussian process is ultraslow [74], 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 [2,47].

In this work, we let the actual value of  $\alpha$  depend on the mode the forager is in. The bimodal search consists of an extensive search mode with parameter  $\alpha$  and an intensive search with parameter  $\alpha'$ . 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  $\alpha' = 3$  (i.e. 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. [75–77] 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 [2]. While such composite random walks have been found to accommodate higher search efficiencies for single foragers [73,77], to the best of our knowledge such composite Lévy searches have not been studied extensively in group foraging scenarios (but see [5]).

In our bimodal Lévy search, the intensive search mode can at any point in time be truncated with probability  $p_\beta$ , 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 [78,79], 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

$$p_\beta(d_0) = 1 - \exp\left(-\frac{\beta d_0}{\ell_0}\right), \tag{3}$$



**Fig. 2.** (a) Wrapped Cauchy distribution  $f_{WC}$  for different shape parameters  $\rho$  with center angle  $\pi/2$ . (b) Simplified typical attraction pattern for a focal forager (●) getting attracted to a successful forager (○) 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  $\rho$  are indicated, and note that as the attracted forager gets closer the more uniform sampling of the travel angle.

where  $\beta$  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  $\beta$ .

Essentially, the switching parameter  $\beta$  determines to what extent a forager should 'exploit' the current region, assumed by the forager to be rich in resources (see also [68,77]). Lower values of  $\beta$  indicate long intensive searches, while higher values of  $\beta$  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 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 [68].

#### 4. 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 [69,80–84], 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 [10], fish [11], bats [19,45], seabirds [13,81,85,86] and gazelles [69]. It relies on use of public information [82,87,88], 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  $\alpha$  [89]. Note here that attraction considers the same Lévy parameter  $\alpha$  as exploration. The mean of the WCD is the angle between the focal forager and the nearest successful conspecific (the attractor). The shape parameter  $\rho$  of the WCD depends on the distance towards the nearest attractor  $d_{near}$  (see Fig. 2). More specifically, we define

$$\rho = \left( \frac{d_{near}}{r} \right)^{\frac{1}{2}}. \tag{4}$$

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. (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)), 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. [90]. Moreover, such hierarchical structures are indeed very common in natural systems [91–93], and leader-follower relationships have been observed to naturally emerge [94–97]. 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. [90] 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 [98–100]. 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.

## 5. 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. 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. [5,69,101–105]). 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 [78], 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.

### 5.1. A single forager in a fractal landscape

As 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  $\alpha$ , for different resource distributions defined by  $\gamma$ . Note that optimality here indicates a strategy (i.e., a particular choice of  $\alpha$ ) 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 [1,2]). This gives the search efficiency as

$$\eta = \frac{k}{d}, \quad (5)$$

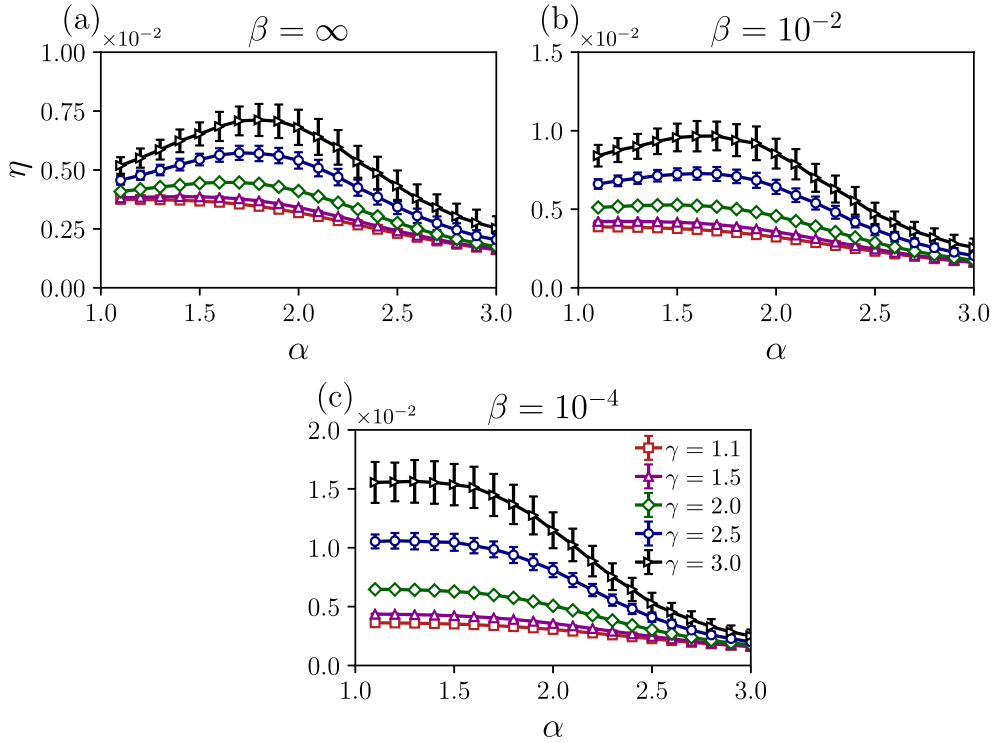
where  $k$  is the number of resources detected by the forager while traveling a distance of  $d$ . Since we truncate the search when a fixed number of resources have been detected, the search efficiency essentially captures how much distance the forager had to traverse during the foraging task.

Let us set  $\beta = \infty$  and thereby recover the unimodal Lévy search that does not adapt its parameter  $\alpha$ , as the switching probability  $p_\infty = 1$  as per Eq. (3) (see also Appendix A). Results are indicated in Fig. 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  $\gamma$  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. [49].

In contrast, when the switching parameter  $\beta$  is finite, we observe that more ballistic motion is favored by the forager (Fig. 3b,c). Most notably, when the switching parameter  $\beta$  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. 3c). It is critical to note that the value of the search efficiency increases as intensive searches are sufficiently long, especially when the resource landscape is highly clustered. This indicates that the adaptive search with finite  $\beta$  is a more efficient strategy than the unimodal Lévy search with  $\beta = \infty$ . Obviously, the switching behavior of the forager is only beneficial when the resources are sufficiently clustered, leading to foragers assuming *a priori* that the 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 [106], 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,  $\beta$  – to some degree – defines 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  $\beta$ , depending on the resource landscape defined by  $\gamma$ , and, as we shall show in Fig. 5, these are indeed observed in our model. More specifically, the optimal value



**Fig. 3.** Search efficiency  $\eta$  versus the  $\alpha$  for a single forager ( $N = 1$ ) performing adaptive Lévy searches for different values of  $\beta$ . Resources are placed using a scale-free distribution with Lévy parameter  $\gamma$ . (a)  $\eta$  for the free Lévy walk, i.e. no intensive search (see Appendix A), versus  $\alpha$ . (b)  $\eta$  for adaptive (bimodal) Lévy searches with (relatively) short intensive searches, and (c) with longer intensive searches. Note the difference of the value of  $\eta$ , where adaptive Lévy walks with  $\beta \ll \infty$  have overall higher search efficiencies than when  $\beta = \infty$ . Error bars represent 1 standard deviation.

$\beta^*$  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 5.2).

It is important to note that most animals can estimate local resource distributions to some degree [75,107,108], and can often react accordingly, meaning that, in reality, the optimal value of  $\beta$  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, but is to be considered valuable future work.

### 5.2. A non-communicating group of foragers

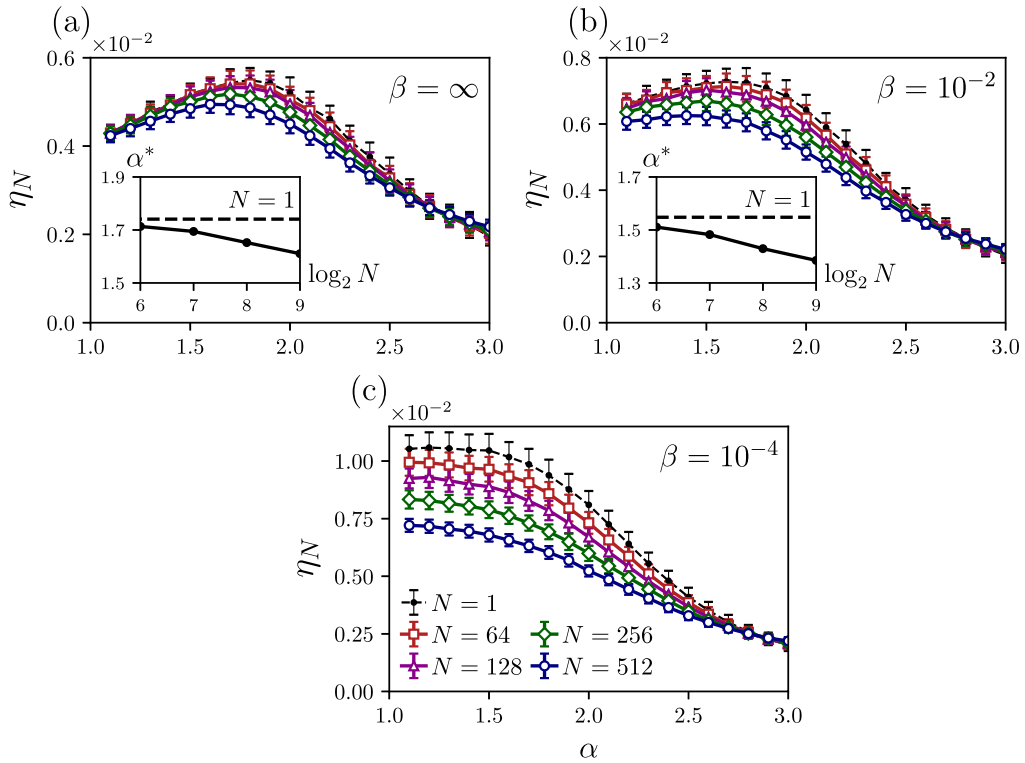
Next, let us consider the bimodal Lévy search in a group of foragers ( $N > 1$ ), wherein no attraction is included, i.e.  $r = 0$ . Such a system is useful to consider, as it provides a baseline with which to compare when studying the benefits of group behavior. Note that although such a system does 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 2), 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 [49]).

#### 5.2.1. The 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  $\eta_N$ . 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

$$\eta_N = \frac{1}{N} \sum_i \frac{k_i}{d_i}, \tag{6}$$

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



**Fig. 4.** Group search efficiency  $\eta_N$  for a non-communicating group of foragers ( $r = 0$ ), versus the Lévy parameter  $\alpha$  for several switching parameters  $\beta$  and a fixed clustered resource distribution with  $\gamma = 2.5$ . Dashed line with black bullets ( $\bullet$ ) represents the search efficiency  $\eta$  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  $\eta_N$  increases as  $\beta$  decreases, indicating that adaptive searches increase the group search efficiency. Insets indicate optimal  $\alpha^*$  for the extensive search, where  $\alpha^* \rightarrow 1$  as  $\beta$  decreases. Intensive searches were executed with  $\alpha' = 3$ . Error bars represent 1 standard deviation.

search efficiency has been used when studying collective systems [5], 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.

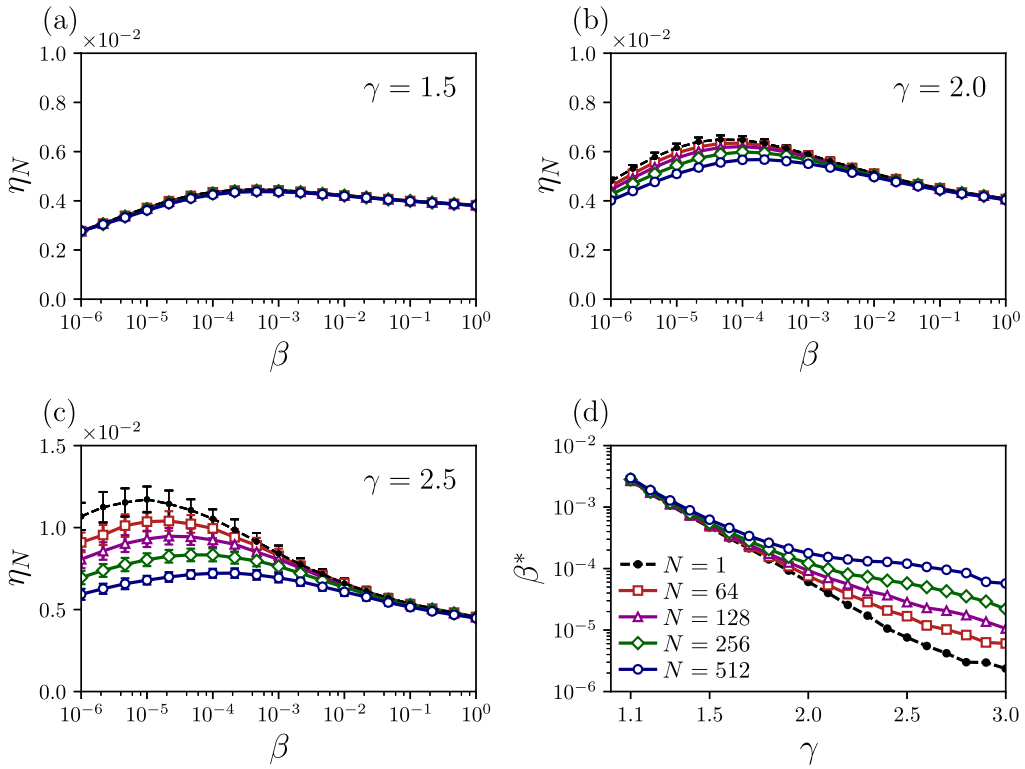
The group search efficiency  $\eta_N$  depends heavily on the individual behavior and interactions between foragers, but additionally depends on the *relative resource density*. This relative measure defines a level of resource availability relative to the number of foragers in the environment. Since 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.

### 5.2.2. Effects of group size on group search efficiency

When studying the effects of the implicit competition, we see similar effects as when studying single foragers systems, in that the optimal extensive search becomes ballistic as  $\beta$  becomes sufficiently small (Fig. 4). More interestingly, group search efficiencies are lower across the entire range of  $\alpha$  compared to a single forager, due to competition for resources. Thus, as group sizes increase, group search efficiencies decrease. Additionally, the search efficiencies for unimodal searches ( $\beta = \infty$ , inset Fig. 4a) and bimodal searches with short intensive searches ( $\beta = 10^{-2}$ , inset Fig. 4b) for groups with  $N > 1$ , display maxima at lower values of  $\alpha$  than when  $N = 1$ . This indeed implies that individuals experience resources to be more sparsely distributed due to others simultaneously foraging destructively [49]. As a result, more diffusive search strategies are, on average, more efficient.

As our results for a single forager ( $N = 1$ , see Section 5.1) 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. 5, we plot the (group) search efficiency for a non-communicating group of foragers for different levels of resource clustering. These results indicate that, when the environment displays little clustering (for  $\gamma = 1.5$ , Fig. 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  $\gamma$  increases, dependence of the group search efficiency on group size becomes apparent. When  $\gamma$  increases while group sizes are large, on-patch competition becomes more fierce, and as a result the optimal value for  $\beta$  is larger compared to when group sizes are smaller (Fig. 5d). This indicates that group members benefit from shortening their intensive searches,





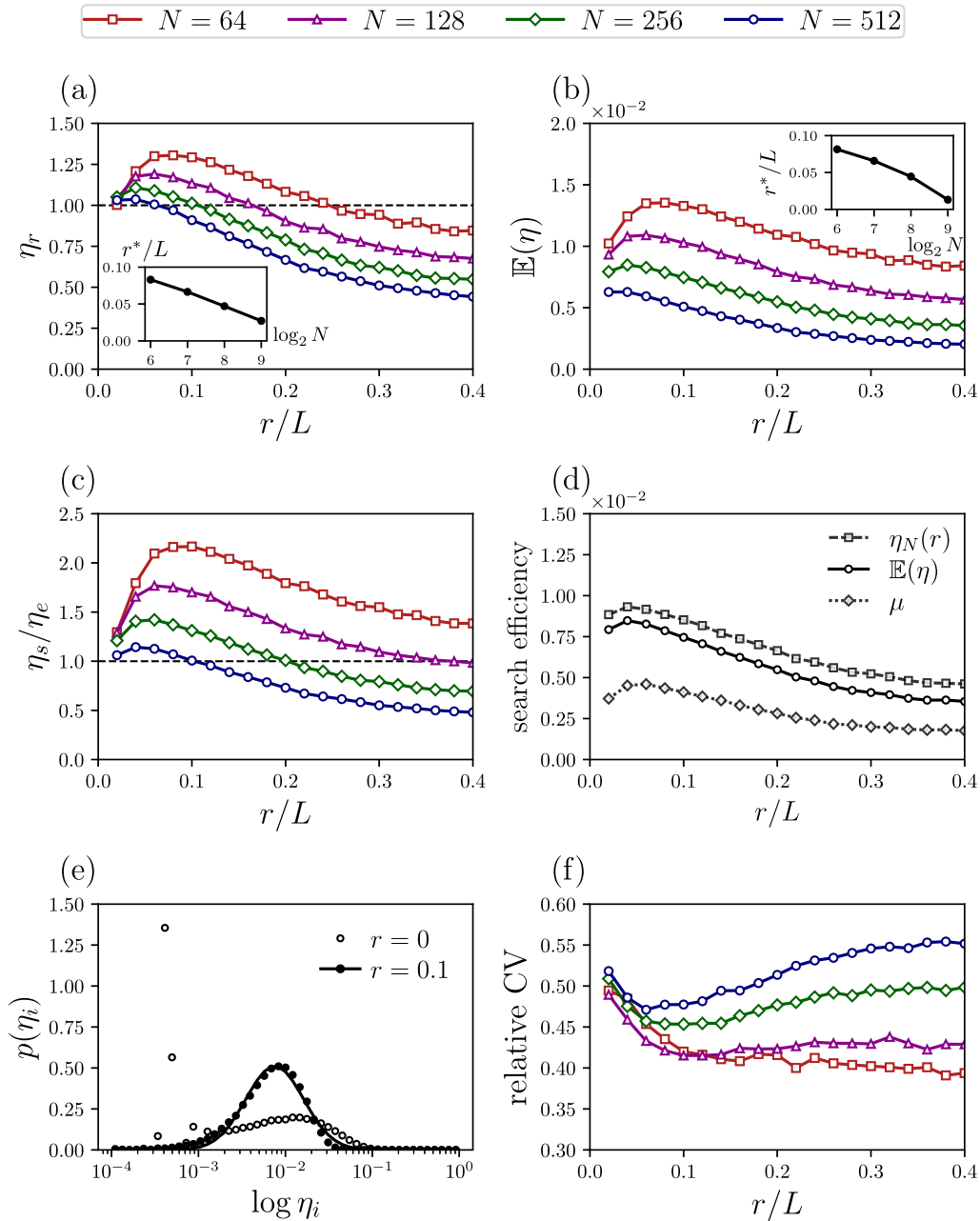
**Fig. 5.** Group search efficiency  $\eta_N$  for a non-communicating group of foragers ( $r = 0$ ) versus the switching parameter  $\beta$ , for several group sizes  $N$  and different levels of resource clustering  $\gamma$ . Dashed line with black bullets ( $\bullet$ ) represent a single forager ( $N = 1$ ) 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  $\gamma$ , 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  $\beta$  that maximizes the (group) search efficiency  $\eta_N$  versus  $\gamma$ , denoted as  $\beta^*$ . Optimal values  $\beta^*$  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  $\beta$  (and  $\beta^*$ ) indicate longer intensive searches, a shift towards shorter intensive searches is observed as group sizes increase and resources become more clustered (see text).

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.

### 5.2.3. Distribution of individual resource intake

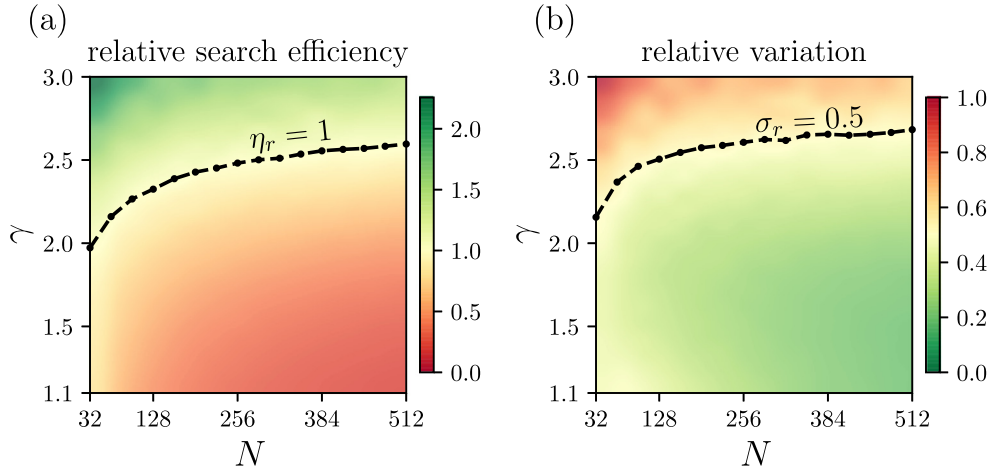
As previously mentioned, when computing the group search efficiency as the group average, this average does not always reflect the underlying distribution of resource encounters. In reality, resource intake distributions become increasingly skewed towards the lucky few who detected dense patches early in the foraging task when resources are significantly clustered (see Appendix B, Fig. B.10). 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. 6e and Fig. B.10), 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  $\gamma$  increases, and subsequently increases the empirical variation (standard deviation) over resource intake rates (Fig. 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. 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  $\beta$  diminish as patches become increasingly dense, as is the case for large enough  $\gamma$ . 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  $\beta$ ).



**Fig. 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  $\eta_r$  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  $\eta_s/\eta_e$  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  $\mu$ , 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  $\eta_i$  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.

Furthermore, we note that the rising inequality can be captured by computing inequality measures [109]. We compute Gini coefficients (see Appendix B for more details) and note that as  $\gamma$  increases, so does the Gini coefficient (see Fig. B.9). More specifically, these high valued Gini coefficients correspond to high inequality in resource intake (large variation). Values of the Gini coefficient are larger when group sizes increase, displaying increased inequality in resource intake rates in larger groups.



**Fig. 7.** Benefits of joining nearby conspecifics for different resource landscapes  $\gamma$  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  $\eta_r$ , computed through Eq. (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  $\sigma_r$  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  $\sigma_r$  serves 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  $\gamma$ .

### 5.3. Group foraging for $r > 0$

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 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 (e.g.  $\beta = 10^{-4}$ ) such that joining becomes feasible. Recall that  $\beta$  modulates the duration of a foragers being attracted, thus choosing large values of  $\beta$  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 resources anymore, 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  $\beta$  such that time ranges over which foragers can effectively join nearby neighbors are sufficiently long. A more intricate study on the effects of  $\beta$  on the effective joining range is considered to be out of the scope of this work.

#### 5.3.1. Group search efficiency

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

$$\eta_r = \frac{\eta_N(r)}{\eta_N}, \tag{7}$$

where  $\eta_N$  is the group search efficiency from the bimodal search with  $r = 0$  as in Eq. (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 have plotted the relative group search efficiency for a clustered resource landscape versus the joining range in Fig. 6a. We note that small populations of foragers have a wide range 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. 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  $\gamma$  and  $N$  in Fig. 7a, 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. 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 small 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  $\eta_e$ . 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  $\eta_s$ . By plotting the ratio of these efficiencies in Fig. 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.

### 5.3.2. Joining promotes intake equality

While attraction to successful conspecifics might not always maximize the groups search efficiency defined in Eq. (6), it is important to note that the distribution over resource intake equalizes as the log-normal distribution becomes a better fit (Fig. 6e, Fig. B.10), and variation in resource intake rates decreases (Fig. 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. B.9b,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 (Fig. 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. 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 [16]. Finally, we mention that joining ranges should not be too short ( $r/L \ll 1$ ), as the system then converges to the non-interacting system for which results are as discussed earlier.

### 5.4. When is joining beneficial while foraging ?

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 [13,16,25,110]. 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. 7a, we show the regions over which joining others becomes 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. 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 intermittent 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. 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.

## 6. 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  $\alpha$ . 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, a group does not necessarily need to optimize group-level search efficiencies, rather than providing each individual more guaranteed 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 depends greatly 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  $\beta$ , adaptive strategies are observed in natural systems [20]. For example,  $\beta$  can be adapted based on the number of nearby foragers, resembling quorum responses [111, 112] and consensus models [113–115]. 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 [104, 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 [4, 103, 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 [53]. Such truncated Lévy searches have been studied in the context of attraction [5] and memory [79]. Furthermore, diffusion characteristics, and thereby foraging efficiencies, are highly influenced by the resource landscape [72]. 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 any memory component that foraging individuals often possess [79,108,124–126], where intricate memory models were observed in multiple 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)), serves as an extremely primitive memory model that considers foragers that approximate local resource densities (see also [49,131]). 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 5.4 – are not expected to be the only driving forces behind group formation [4]. For example, group size might increase foraging success [9,133], 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  $\gamma$  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 be of 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 have profound impacts on the survival of foraging species, and should undoubtedly be included in future models.

This work has introduced an agent-based model for group foraging in fractal resource landscapes. Depending on group sizes and resource distributions, we show 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.

### CRedit authorship contribution statement

**Johannes Nauta:** Conceptualization, Methodology, Software, Formal analysis, Writing – original draft, Visualization. **Pieter Simoens:** Conceptualization, Supervision, Writing – review & editing. **Yara Khaluf:** Conceptualization, Writing – review & editing, Supervision.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Appendix A. Influence of $\beta$ on intensive searches

Recall the switching probability defined in Eq. (3) as

$$p_\beta(L_0) = 1 - \exp\left(\frac{-\beta L_0}{\ell_0}\right) \tag{A.1}$$

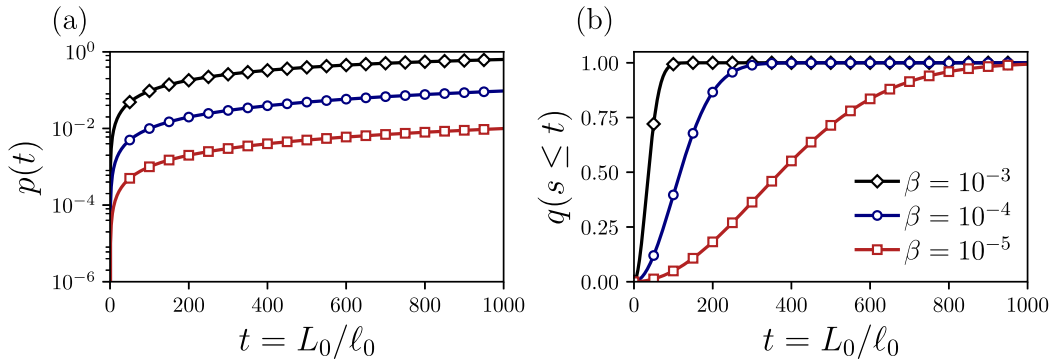
To further consolidate the effects of  $\beta$  on the expected lengths of the intensive search, we can write the probability of exiting the intensive search after having traveled a distance  $L_0$  without resource detection, as

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

In this form,  $t$  represents the (discrete) time, i.e. number of steps, needed to travel a distance of  $L_0$  with increments of  $\ell_0$ . Then, the cumulative of this distribution defines the probability of needing *at most*  $t$  steps before truncation

$$q(s \leq t) = \int_0^t ds (1 - \exp(-\beta s)) \exp\left(-\frac{1}{2}\beta(s-1)s\right). \tag{A.3}$$

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 (see Fig. A.8).

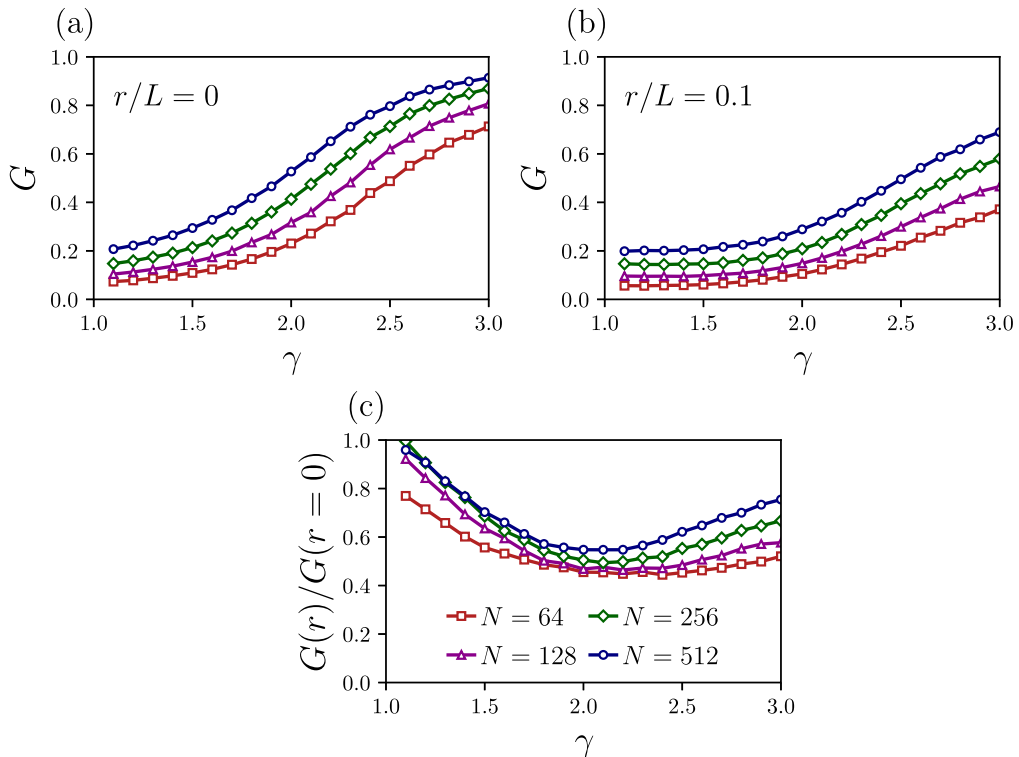


**Fig. A.8.** Plots on the influence of  $\beta$  on the length (number of steps) of intensive searches. (a) Probability of switching from intensive search to extensive search after  $t$  steps of no resource detection. (b) Cumulative density function of taking at most  $t$  steps until truncation of the intensive search. Note that (relatively) large values of  $\beta$  result in fast truncation of intensive searches, while smaller values facilitate longer intensive searches.

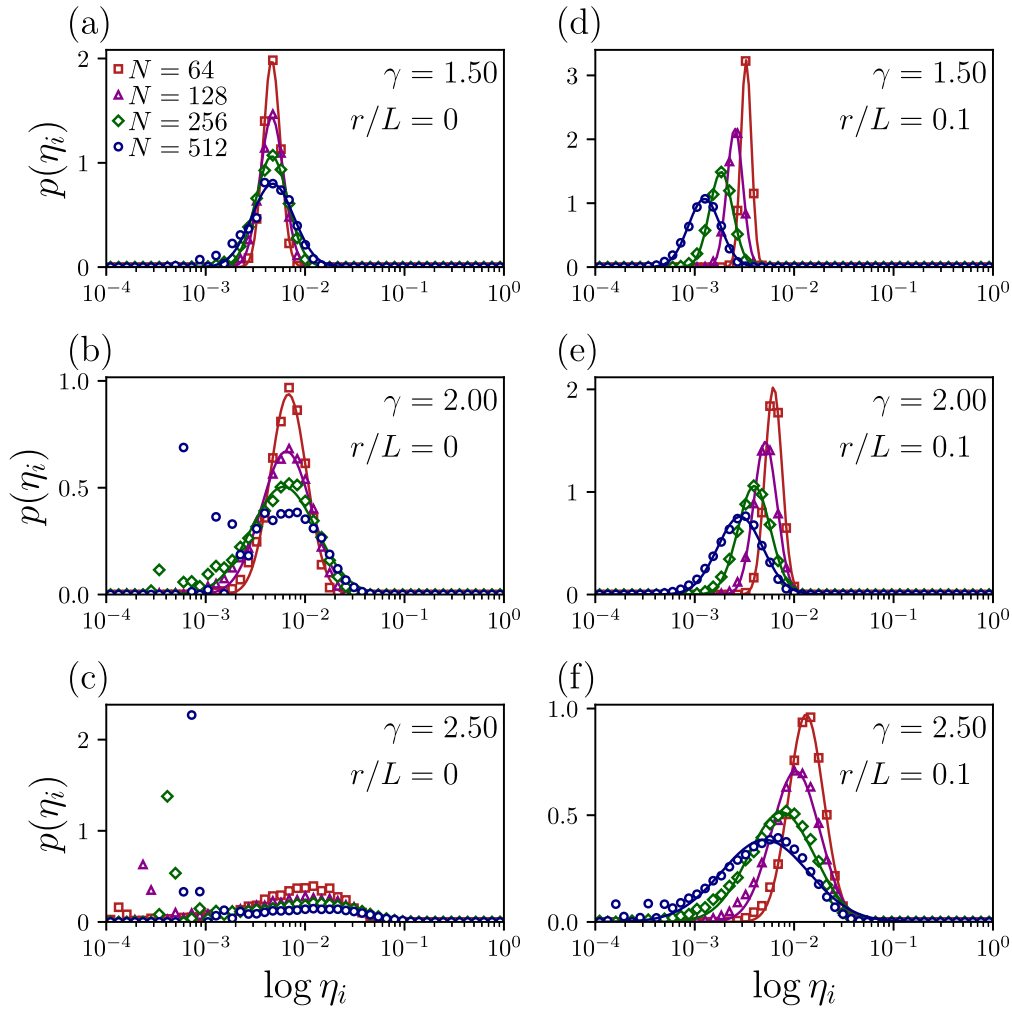
**Appendix B. Details on the resource intake distribution**

Recall that intraspecific competition manifests itself in rising inequality within the distribution of resource intake among foragers (see Sections 5.2 and 5.3). As a way of measuring this inequality, we use the well-known Gini coefficient [109,147]

$$G = \frac{\sum_{i=1}^N \sum_{j=1}^N |k_i - k_j|}{2N \sum_{i=1}^N k_i}. \tag{B.1}$$



**Fig. B.9.** Gini coefficient  $G$  versus the resource Lévy parameter  $\gamma$ , for different group sizes  $N$ . (a) Displays  $G$  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. B.10). Results are obtained for fixed bi- and trimodal Lévy searches with  $\alpha = 1.1$  and  $\beta = 10^{-4}$ .



**Fig. B.10.** Distribution over search efficiencies of individuals for different group sizes, in resource landscapes with different levels of clustering (see Fig. 1). For each forager  $i$ , the search efficiency  $\eta_i$  is computed as in Eq. (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  $\beta = 10^{-4}$ .

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  $\gamma$  in Fig. B.9a,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 these results are illustrated in Fig. B.10, 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 fail to explain the data due to the existence of a large fraction of foragers finding little to no resources (i.e. high  $G$ , see Fig. B.9a). 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. B.10c,f).

## References

- [1] G.M. Viswanathan, S.V. Buldyrev, S. Havlin, M. Da Luz, E. Raposo, H.E. Stanley, Optimizing the success of random searches, *Nature* 401 (6756) (1999) 911.
- [2] G.M. Viswanathan, M.G. Da Luz, E.P. Raposo, H.E. Stanley, *The Physics of Foraging: an Introduction to Random Searches and Biological Encounters*, Cambridge University Press, 2011.
- [3] M.E. Wosniack, M.C. Santos, E.P. Raposo, G.M. Viswanathan, M.G.E. da Luz, Robustness of optimal random searches in fragmented environments, *Phys. Rev. E* 91 (2015) 052119.
- [4] J. Krause, G.D. Ruxton, *Living in Groups*, Oxford University Press, 2002.
- [5] K. Bhattacharya, T. Vicsek, Collective foraging in heterogeneous landscapes, *J. R. Soc. Interface* 11 (100) (2014) 20140674.
- [6] T. Pitcher, A. Magurran, I. Winfield, Fish in larger shoals find food faster, *Behav. Ecol. Sociobiol.* 10 (2) (1982) 149–151.
- [7] J.C. Haney, K.M. Fristrup, D.S. Lee, Geometry of visual recruitment by seabirds to ephemeral foraging flocks, *Ornis Scand.* (1992) 49–62.
- [8] L.-A. Giraldeau, G. Beauchamp, Food exploitation: searching for the optimal joining policy, *Trends Ecol. Evol.* 14 (3) (1999) 102–106.
- [9] A.M. McInnes, C. McGeorge, S. Ginsberg, L. Pichegru, P.A. Pistorius, Group foraging increases foraging efficiency in a piscivorous diver, the African penguin, *R. Soc. Open Sci.* 4 (9) (2017) 170918.
- [10] S.S. Ding, L.J. Schumacher, A.E. Javer, R.G. Endres, A.E. Brown, Shared behavioral mechanisms underlie *C. elegans* aggregation and swarming, *ELife* 8 (2019) e43318.
- [11] R. Harpaz, E. Schneidman, Social interactions drive efficient foraging and income equality in groups of fish, *Elife* 9 (2020) e56196.
- [12] P. Monaghan, N.B. Metcalfe, Group foraging in wild brown hares: effects of resource distribution and social status, *Anim. Behav.* 33 (3) (1985) 993–999.
- [13] M. Hake, J. Ekman, Finding and sharing depletable patches: when group foraging decreases intake rates, *Ornis Scand.* (1988) 275–279.
- [14] E. Ranta, H. Rita, K. Lindstrom, Competition versus cooperation: success of individuals foraging alone and in groups, *Amer. Nat.* 142 (1) (1993) 42–58.
- [15] H. Rita, E. Ranta, Competition in a group of equal foragers, *Amer. Nat.* 152 (1) (1998) 71–81.
- [16] G. Beauchamp, Does group foraging promote efficient exploitation of resources? *Oikos* 111 (2) (2005) 403–407.
- [17] G. Beauchamp, Effect of group size on feeding rate when patches are exhaustible, *Ethology* 113 (1) (2007) 57–61.
- [18] R. Svanbäck, D.I. Bolnick, Intraspecific competition drives increased resource use diversity within a natural population, *Proc. R. Soc. B: Biol. Sci.* 274 (1611) (2007) 839–844.
- [19] N. Cvikel, K.E. Berg, E. Levin, E. Hurme, I. Borissov, A. Boonman, E. Amichai, Y. Yovel, Bats aggregate to improve prey search but might be impaired when their density becomes too high, *Curr. Biol.* 25 (2) (2015) 206–211, <http://dx.doi.org/10.1016/j.cub.2014.11.010>.
- [20] G.D. Ruxton, C. Fraser, M. Broom, An evolutionarily stable joining policy for group foragers, *Behav. Ecol.* 16 (5) (2005) 856–864.
- [21] G. Ruxton, S. Hall, W. Gurney, Attraction toward feeding conspecifics when food patches are exhaustible, *Amer. Nat.* 145 (4) (1995) 653–660.
- [22] G. Beauchamp, L.-A. Giraldeau, Group foraging revisited: information sharing or producer-scrounger game? *Amer. Nat.* 148 (4) (1996) 738–743.
- [23] W.L. Vickery, L.-A. Giraldeau, J.J. Templeton, D.L. Kramer, C.A. Chapman, Producers, scroungers, and group foraging, *Amer. Nat.* 137 (6) (1991) 847–863.
- [24] T. Caraco, L.-A. Giraldeau, Social foraging: producing and scrounging in a stochastic environment, *J. Theoret. Biol.* 153 (4) (1991) 559–583.
- [25] C.W. Clark, M. Mangel, Foraging and flocking strategies: information in an uncertain environment, *Amer. Nat.* 123 (5) (1984) 626–641.
- [26] D. Naug, J. Wenzel, Constraints on foraging success due to resource ecology limit colony productivity in social insects, *Behav. Ecol. Sociobiol.* 60 (1) (2006) 62–68.
- [27] C.J. Barnard, R.M. Sibly, Producers and scroungers: a general model and its application to captive flocks of house sparrows, *Anim. Behav.* 29 (2) (1981) 543–550.
- [28] G. Beauchamp, A spatial model of producing and scrounging, *Anim. Behav.* 76 (6) (2008) 1935–1942.
- [29] A.J. King, N.J. Isaac, G. Cowlshaw, Ecological, social, and reproductive factors shape producer–scrounger dynamics in baboons, *Behav. Ecol.* 20 (5) (2009) 1039–1049.
- [30] J.W. Jolles, L. Ostojić, N.S. Clayton, Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *corvus frugilegus*, *Anim. Behav.* 85 (6) (2013) 1261–1269.
- [31] K.J. Mathot, L.-A. Giraldeau, Within-group relatedness can lead to higher levels of exploitation: a model and empirical test, *Behav. Ecol.* 21 (4) (2010) 843–850.
- [32] P. Fauchald, Foraging in a hierarchical patch system, *Amer. Nat.* 153 (6) (1999) 603–613.
- [33] C.J. Johnson, M.S. Boyce, R. Mulders, A. Gunn, R.J. Gau, H.D. Cluff, R.L. Case, Quantifying patch distribution at multiple spatial scales: Applications to wildlife-habitat models, *Landsc. Ecol.* 19 (8) (2004) 869–882.
- [34] S. Kéfi, M. Rietkerk, C.L. Alados, Y. Pueyo, V.P. Papanastasis, A. ElAich, P.C. De Ruiter, Spatial vegetation patterns and imminent desertification in mediterranean arid ecosystems, *Nature* 449 (7159) (2007) 213–217, <http://dx.doi.org/10.1038/nature06111>.
- [35] T.M. Scanlon, K.K. Caylor, S.A. Levin, I. Rodriguez-Iturbe, Positive feedbacks promote power-law clustering of kalahari vegetation, *Nature* 449 (7159) (2007) 209–212, <http://dx.doi.org/10.1038/nature06060>.
- [36] R.W. Russell, G.L. Hunt, K.O. Coyle, R.T. Cooney, Foraging in a fractal environment: spatial patterns in a marine predator-prey system, *Landsc. Ecol.* 7 (3) (1992) 195–209, <http://dx.doi.org/10.1007/BF00133310>.
- [37] A. Tsuda, Fractal distribution of an oceanic copepod *neocalanus cristatus* in the subarctic pacific, *J. Oceanogr.* 51 (3) (1995) 261–266.
- [38] K.A. With, A.W. King, Dispersal success on fractal landscapes: a consequence of lacunarity thresholds, *Landsc. Ecol.* 14 (1) (1999) 73–82, <http://dx.doi.org/10.1023/A:1008030215600>.
- [39] L.P. Garrison, W. Michaels, J.S. Link, M.J. Fogarty, Spatial distribution and overlap between ichthyoplankton and pelagic fish and squids on the southern flank of georges bank, *Fisheries Oceanography* 11 (5) (2002) 267–285.
- [40] M.S. Hoddle, The effect of prey species and environmental complexity on the functional response of *Franklinothrips orizabensis*: a test of the fractal foraging model, *Ecol. Entomol.* 28 (3) (2003) 309–318, <http://dx.doi.org/10.1046/j.1365-2311.2003.00518.x>.
- [41] P. Fréon, P. Cury, L. Shannon, C. Roy, Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review, *Bull. Mar. Sci.* 76 (2) (2005) 385–462.
- [42] D.W. Sims, E.J. Southall, N.E. Humphries, G.C. Hays, C.J. Bradshaw, J.W. Pitchford, A. James, M.Z. Ahmed, A.S. Brierley, M.A. Hindell, et al., Scaling laws of marine predator search behaviour, *Nature* 451 (7182) (2008) 1098.
- [43] M. Wheatley, Domains of scale in forest-landscape metrics: Implications for species-habitat modeling, *Acta Oecologica* 36 (2) (2010) 259–267.
- [44] Y. Khaluf, E. Ferrante, P. Simoens, C. Huepe, Scale invariance in natural and artificial collective systems: a review, *J. R. Soc. Interface* 14 (136) (2017) 20170662, <http://dx.doi.org/10.1098/rsif.2017.0662>.

- [45] K. Egert-Berg, E.R. Hurme, S. Greif, A. Goldstein, L. Harten, J.J. Flores-Martínez, A.T. Valdés, D.S. Johnston, O. Eitan, I. Borissov, et al., Resource ephemerality drives social foraging in bats, *Curr. Biol.* 28 (22) (2018) 3667–3673.
- [46] G.M. Viswanathan, V. Afanasyev, S. Buldyrev, E. Murphy, P. Prince, H.E. Stanley, Lévy flight search patterns of wandering albatrosses, *Nature* 381 (6581) (1996) 413–415.
- [47] V. Zaburdaev, S. Denisov, J. Klafter, Lévy walks, *Rev. Modern Phys.* 87 (2) (2015) 483.
- [48] E.P. Raposo, S.V. Buldyrev, M.G.E. da Luz, M.C. Santos, H.E. Stanley, G.M. Viswanathan, Dynamical robustness of Lévy search strategies, *Phys. Rev. Lett.* 91 (2003) 240601.
- [49] A. Ferreira, E. Raposo, G. Viswanathan, M. Da Luz, The influence of the environment on Lévy random search efficiency: fractality and memory effects, *Physica A* 391 (11) (2012) 3234–3246.
- [50] M. Wosniack, E. Raposo, G. Viswanathan, M. da Luz, Efficient search of multiple types of targets, *Phys. Rev. E* 92 (6) (2015) 062135.
- [51] S. Benhamou, How many animals really do the Lévy walk? *Ecology* 88 (8) (2007) 1962–1969.
- [52] A.M. Edwards, Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals, *Ecology* 92 (6) (2011) 1247–1257.
- [53] A. James, M.J. Plank, A.M. Edwards, Assessing Lévy walks as models of animal foraging, *J. R. Soc. Interface* 8 (62) (2011) 1233–1247.
- [54] S. Petrovskii, A. Mashanova, V.A. Jansen, Variation in individual walking behavior creates the impression of a Lévy flight, *Proc. Natl. Acad. Sci.* 108 (21) (2011) 8704–8707.
- [55] G.H. Pyke, Understanding movements of organisms: it's time to abandon the Lévy foraging hypothesis, *Methods Ecol. Evol.* 6 (1) (2015) 1–16.
- [56] A.M. Reynolds, N.T. Ouellette, Swarm dynamics may give rise to Lévy flights, *Sci. Rep.* 6 (1) (2016) 1–8.
- [57] G. Ariel, A. Rabani, S. Benisty, J.D. Partridge, R.M. Harshey, A. Be'Er, Swarming bacteria migrate by Lévy walk, *Nature Commun.* 6 (1) (2015) 1–6.
- [58] S. Huda, B. Weigelin, K. Wolf, K.V. Tretiakov, K. Polev, G. Wilk, M. Iwasa, F.S. Emami, J.W. Narojczyk, M. Banaszak, et al., Lévy-like movement patterns of metastatic cancer cells revealed in microfabricated systems and implicated in vivo, *Nature Commun.* 9 (1) (2018) 1–11.
- [59] T.H. Harris, E.J. Banigan, D.A. Christian, C. Konradt, E.D.T. Wojno, K. Norose, E.H. Wilson, B. John, W. Weninger, A.D. Luster, et al., Generalized Lévy walks and the role of chemokines in migration of effector CD8+ T cells, *Nature* 486 (7404) (2012) 545–548.
- [60] N.E. Humphries, N. Queiroz, J.R. Dyer, N.G. Pade, M.K. Musyl, K.M. Schaefer, D.W. Fuller, J.M. Brunnschweiler, T.K. Doyle, J.D. Houghton, et al., Environmental context explains Lévy and Brownian movement patterns of marine predators, *Nature* 465 (7301) (2010) 1066–1069.
- [61] A.M. Reynolds, A.D. Smith, R. Menzel, U. Greggers, D.R. Reynolds, J.R. Riley, Displaced honey bees perform optimal scale-free search flights, *Ecology* 88 (8) (2007) 1955–1961.
- [62] S. Focardi, P. Montanaro, E. Pecchioli, Adaptive Lévy walks in foraging fallow deer, *PLoS One* 4 (8) (2009) e6587.
- [63] A.M. Foley, R.W. DeYoung, D.G. Hewitt, M.W. Hellickson, K.L. Gee, D.B. Wester, M.A. Lockwood, K.V. Miller, Purposeful wanderings: mate search strategies of male white-tailed deer, *J. Mammal.* 96 (2) (2015) 279–286.
- [64] D.A. Raichlen, B.M. Wood, A.D. Gordon, A.Z. Mabulla, F.W. Marlowe, H. Pontzer, Evidence of Lévy walk foraging patterns in human hunter-gatherers, *Proc. Natl. Acad. Sci.* 111 (2) (2014) 728–733.
- [65] M. Vahabi, J.H. Schulz, B. Shokri, R. Metzler, Area coverage of radial Lévy flights with periodic boundary conditions, *Phys. Rev. E* 87 (4) (2013) 042136.
- [66] B. Guinard, A. Korman, Intermittent inverse-square Lévy walks are optimal for finding targets of all sizes, *Sci. Adv.* 7 (15) (2021) eabe8211.
- [67] O. Bénichou, C. Loverdo, M. Moreau, R. Voituriez, Two-dimensional intermittent search processes: An alternative to Lévy flight strategies, *Phys. Rev. E* 74 (2) (2006) 020102.
- [68] A. Reynolds, Adaptive Lévy walks can outperform composite Brownian walks in non-destructive random searching scenarios, *Physica A* 388 (5) (2009) 561–564.
- [69] R. Martínez-García, J.M. Calabrese, T. Mueller, K.A. Olson, C. López, Optimizing the search for resources by sharing information: Mongolian gazelles as a case study, *Phys. Rev. Lett.* 110 (24) (2013) 248106.
- [70] C.J. Torney, A. Berdahl, I.D. Couzin, Signalling and the evolution of cooperative foraging in dynamic environments, *PLoS Comput. Biol.* 7 (9) (2011).
- [71] N. Kenkel, A. Irwin, Fractal analysis of dispersal, *Abstr. Bot.* (1994) 79–84.
- [72] O. Miramontes, D. Boyer, F. Bartumeus, The effects of spatially heterogeneous prey distributions on detection patterns in foraging seabirds, *PLoS One* 7 (4) (2012) e34317.
- [73] M. Plank, A. James, Optimal foraging: Lévy pattern or process? *J. R. Soc. Interface* 5 (26) (2008) 1077–1086.
- [74] R.N. Mantegna, H.E. Stanley, Stochastic process with ultraslow convergence to a Gaussian: The truncated Lévy flight, *Phys. Rev. Lett.* 73 (1994) 2946–2949.
- [75] S. Benhamou, Efficiency of area-concentrated searching behaviour in a continuous patchy environment, *J. Theoret. Biol.* 159 (1) (1992) 67–81.
- [76] H. Weimerskirch, Are seabirds foraging for unpredictable resources? *Deep Sea Res. II: Top. Stud. Oceanogr.* 54 (3) (2007) 211–223.
- [77] B.C. Nolting, T.M. Hinkelman, C.E. Brassil, B. Tenhumberg, Composite random search strategies based on non-directional sensory cues, *Ecol. Complex.* 22 (2015) 126–138.
- [78] K. Zhao, R. Jurdak, J. Liu, D. Westcott, B. Kusy, H. Parry, P. Sommer, A. McKeown, Optimal Lévy-flight foraging in a finite landscape, *J. R. Soc. Interface* 12 (104) (2015) 20141158.
- [79] J. Nauta, Y. Khaluf, P. Simoens, Hybrid foraging in patchy environments using spatial memory, *J. R. Soc. Interface* 17 (166) (2020) 20200026.
- [80] A.L. Rand, *Social Feeding Behavior of Birds*, Vol. 36, no. 1, Chicago Natural History Museum, 1954, p. 92.
- [81] M. Gochfeld, J. Burger, Feeding enhancement by social attraction in the sandwich tern, *Behav. Ecol. Sociobiol.* 10 (1) (1982) 15–17.
- [82] B.G. Galef Jr., L.-A. Giraldeau, Social influences on foraging in vertebrates: causal mechanisms and adaptive functions, *Anim. Behav.* 61 (1) (2001) 3–15, <http://dx.doi.org/10.1006/anbe.2000.1557>.
- [83] K. McComb, D. Reby, L. Baker, C. Moss, S. Sayialel, Long-distance communication of acoustic cues to social identity in African elephants, *Anim. Behav.* 65 (2) (2003) 317–329.
- [84] G. Ramos-Fernández, Social communication in a fission-fusion society: do spider monkeys stay in touch with close associates? *Int. J. Primatol.* 26 (5) (2005) 1077–1092.
- [85] F. Götmark, D.W. Winkler, M. Andersson, Flock-feeding on fish schools increases individual success in gulls, *Nature* 319 (6054) (1986) 589–591.
- [86] J.C. Evans, C.J. Torney, S.C. Votier, S.R. Dall, Social information use and collective foraging in a pursuit diving seabird, *PLoS One* 14 (9) (2019) e0222600.
- [87] T.J. Valone, Group foraging, public information, and patch estimation, *Oikos* (1989) 357–363.
- [88] E. Danchin, L.-A. Giraldeau, T.J. Valone, R.H. Wagner, Public information: from nosy neighbors to cultural evolution, *Science* 305 (5683) (2004) 487–491.
- [89] F. Bartumeus, M.G.E. da Luz, G.M. Viswanathan, J. Catalan, Animal search strategies: a quantitative random-walk analysis, *Ecology* 86 (11) (2005) 3078–3087.
- [90] M. Santos, E. Raposo, G. Viswanathan, M. da Luz, Can collective searches profit from Lévy walk strategies? *J. Phys. A* 42 (43) (2009) 434017.
- [91] S. Boinski, P.A. Garber, *On the Move: How and Why Animals Travel in Groups*, University of Chicago Press, 2000.

- [92] L. Conradt, T.J. Roper, Group decision-making in animals, *Nature* 421 (6919) (2003) 155–158.
- [93] M. Nagy, Z. Ákos, D. Biro, T. Vicsek, Hierarchical group dynamics in pigeon flocks, *Nature* 464 (7290) (2010) 890–893.
- [94] A.J. King, C.M. Douglas, E. Huchard, N.J. Isaac, G. Cowlshaw, Dominance and affiliation mediate despotism in a social primate, *Curr. Biol.* 18 (23) (2008) 1833–1838.
- [95] M. Hurwitz, Exploring distributed leadership: A leader–follower collaborative lens, in: *Distributed Leadership*, Springer, 2018, pp. 1–25.
- [96] S.A. Rands, G. Cowlshaw, R.A. Pettifor, J.M. Rowcliffe, R.A. Johnstone, The emergence of leaders and followers in foraging pairs when the qualities of individuals differ, *BMC Evol. Biol.* 8 (1) (2008) 1–17.
- [97] R. Martínez-García, C. López, F. Vazquez, Optimal recruitment strategies for groups of interacting walkers with leaders, *Phys. Rev. E* 91 (2) (2015) 022117.
- [98] G. Ramos-Fernández, D. Boyer, V.P. Gómez, A complex social structure with fission–fusion properties can emerge from a simple foraging model, *Behav. Ecol. Sociobiol.* 60 (4) (2006) 536–549.
- [99] I.D. Couzin, M.E. Laidre, Fission–fusion populations, *Curr. Biol.* 19 (15) (2009) R633–R635.
- [100] C. Sueur, A.J. King, L. Conradt, G. Kerth, D. Lusseau, C. Mettke-Hofmann, C.M. Schaffner, L. Williams, D. Zinner, F. Aureli, Collective decision-making and fission–fusion dynamics: a conceptual framework, *Oikos* 120 (11) (2011) 1608–1617.
- [101] F.-X. Dechaume-Moncharmont, A. Dornhaus, A.I. Houston, J.M. McNamara, E.J. Collins, N.R. Franks, The hidden cost of information in collective foraging, *Proc. R. Soc. B: Biol. Sci.* 272 (1573) (2005) 1689–1695.
- [102] J. Beal, Superdiffusive dispersion and mixing of swarms with reactive Lévy walks, in: *2013 IEEE 7th International Conference on Self-Adaptive and Self-Organizing Systems*, IEEE, 2013, pp. 141–148.
- [103] M. Lihoreau, J. Buhl, M.A. Charleston, G.A. Sword, D. Raubenheimer, S.J. Simpson, Nutritional ecology beyond the individual: a conceptual framework for integrating nutrition and social interactions, *Ecol. Lett.* 18 (3) (2015) 273–286.
- [104] H. Hamann, *Swarm Robotics: A Formal Approach*, Springer, 2018.
- [105] A. Falcón-Cortés, D. Boyer, G. Ramos-Fernández, Collective learning from individual experiences and information transfer during group foraging, *J. R. Soc. Interface* 16 (151) (2019) 20180803.
- [106] D. Campos, F. Bartumeus, E. Raposo, V. Méndez, First-passage times in multiscale random walks: the impact of movement scales on search efficiency, *Phys. Rev. E* 92 (5) (2015) 052702.
- [107] S. Benhamou, P. Bovet, How animals use their environment: a new look at kinesis, *Anim. Behav.* 38 (3) (1989) 375–383.
- [108] C. Bracis, E. Gurarie, B. Van Moorter, R.A. Goodwin, Memory effects on movement behavior in animal foraging, *PLoS One* 10 (8) (2015) e0136057.
- [109] A.B. Atkinson, et al., On the measurement of inequality, *J. Econom. Theory* 2 (3) (1970) 244–263.
- [110] L.-A. Giraldeau, T. Caraco, *Social Foraging Theory*, Vol. 73, Princeton University Press, 2018.
- [111] D.J. Sumpter, The principles of collective animal behaviour, *Philos. Trans. R. Soc. B* 361 (1465) (2006) 5–22.
- [112] A.J. Ward, D.J. Sumpter, I.D. Couzin, P.J. Hart, J. Krause, Quorum decision-making facilitates information transfer in fish shoals, *Proc. Natl. Acad. Sci.* 105 (19) (2008) 6948–6953.
- [113] N.D. McDonald, S.A. Rands, F. Hill, C. Elder, C.C. Ioannou, Consensus and experience trump leadership, suppressing individual personality during social foraging, *Sci. Adv.* 2 (9) (2016) e1600892.
- [114] Y. Khaluf, I. Rausch, P. Simoens, The impact of interaction models on the coherence of collective decision-making: a case study with simulated locusts, in: *International Conference on Swarm Intelligence*, Springer, 2018, pp. 252–263.
- [115] S. Bidari, O. Peleg, Z.P. Kilpatrick, Social inhibition maintains adaptivity and consensus of honeybees foraging in dynamic environments, *R. Soc. Open Sci.* 6 (12) (2019) 191681.
- [116] M. Brabbilla, E. Ferrante, M. Birattari, M. Dorigo, Swarm robotics: a review from the swarm engineering perspective, *Swarm Intell.* 7 (1) (2013) 1–41.
- [117] S.J. Simpson, D. Raubenheimer, *The Nature of Nutrition: A Unifying Framework from Animal Adaptation To Human Obesity*, Princeton University Press, 2012.
- [118] L.M. Aplin, D.R. Farine, R.P. Mann, B.C. Sheldon, Individual-level personality influences social foraging and collective behaviour in wild birds, *Proc. R. Soc. B: Biol. Sci.* 281 (1789) (2014) 20141016.
- [119] A.M. Senior, M. Lihoreau, M.A. Charleston, J. Buhl, D. Raubenheimer, S.J. Simpson, Adaptive collective foraging in groups with conflicting nutritional needs, *R. Soc. Open Sci.* 3 (4) (2016) 150638.
- [120] D. Kengyel, H. Hamann, P. Zahadat, G. Radspieler, F. Wotawa, T. Schmickl, Potential of heterogeneity in collective behaviors: A case study on heterogeneous swarms, in: *International Conference on Principles and Practice of Multi-Agent Systems*, Springer, 2015, pp. 201–217.
- [121] K. Szwajkowska, L.M.-y.-T. Romero, I.B. Schwartz, Collective motions of heterogeneous swarms, *IEEE Trans. Autom. Sci. Eng.* 12 (3) (2015) 810–818.
- [122] A. Clauset, C.R. Shalizi, M.E. Newman, Power-law distributions in empirical data, *SIAM Rev.* 51 (4) (2009) 661–703.
- [123] A. James, J.W. Pitchford, M. Plank, Efficient or inaccurate? Analytical and numerical modelling of random search strategies, *Bull. Math. Biol.* 72 (4) (2010) 896–913.
- [124] D. Boyer, P.D. Walsh, Modelling the mobility of living organisms in heterogeneous landscapes: does memory improve foraging success? *Phil. Trans. R. Soc. A* 368 (1933) (2010) 5645–5659.
- [125] D. Boyer, M.C. Crofoot, P.D. Walsh, Non-random walks in monkeys and humans, *J. R. Soc. Interface* 9 (70) (2011) 842–847.
- [126] A.J. Calhoun, S.H. Chalasani, T.O. Sharpee, Maximally informative foraging by *Caenorhabditis elegans*, *Elife* 3 (2014) e04220.
- [127] F. Dyer, Spatial memory and navigation by honeybees on the scale of the foraging range, *J. Exp. Biol.* 199 (1) (1996) 147–154.
- [128] Y. Winter, K.P. Stich, Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats, *J. Exp. Biol.* 208 (3) (2005) 539–548.
- [129] C.H. Janson, Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*, *Anim. Behav.* 55 (5) (1998) 1229–1243.
- [130] M.P. Tujague, C.H. Janson, Wild capuchin monkeys anticipate the amount of ripe fruit in natural trees, *Anim. Cogn.* 20 (5) (2017) 841–853.
- [131] O. Olsson, J. S. Brown, The foraging benefits of information and the penalty of ignorance, *Oikos* 112 (2) (2006) 260–273.
- [132] L. Riotte-Lambert, S. Benhamou, C. Bonenfant, S. Chamailé-Jammes, Spatial memory shapes density dependence in population dynamics, *Proc. R. Soc. B: Biol. Sci.* 284 (1867) (2017) 20171411.
- [133] K.J. Benoit-Bird, W.W. Au, Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*, *J. Acoust. Soc. Am.* 125 (1) (2009) 125–137, <http://dx.doi.org/10.1121/1.2967480>.
- [134] S. Creel, N.M. Creel, Communal hunting and pack size in african wild dogs, *Lycaon pictus*, *Anim. Behav.* 50 (5) (1995) 1325–1339.
- [135] L.D. Mech, L. Boitani, *Wolves: Behavior, Ecology, and Conservation*, University of Chicago Press, 2007.
- [136] F. Aureli, C.M. Schaffner, C. Boesch, S.K. Bearder, J. Call, C.A. Chapman, R. Connor, A.D. Fiore, R.I. Dunbar, S.P. Henzi, et al., Fission–fusion dynamics: new research frameworks, *Curr. Anthropol.* 49 (4) (2008) 627–654.
- [137] J.S. Brown, Vigilance, patch use and habitat selection: foraging under predation risk, *Evol. Ecol. Res.* 1 (1) (1999) 49–71.
- [138] A.M. Bell, A. Sih, Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*), *Ecol. Lett.* 10 (9) (2007) 828–834.

- [139] J. Cote, S. Fogarty, B. Tymen, A. Sih, T. Brodin, Personality-dependent dispersal cancelled under predation risk, *Proc. R. Soc. B: Biol. Sci.* 280 (1773) (2013) 20132349.
- [140] G. Beauchamp, Vigilance in a selfish herd, *Anim. Behav.* 73 (3) (2007) 445–451.
- [141] G. Beauchamp, Function and structure of vigilance in a gregarious species exposed to threats from predators and conspecifics, *Anim. Behav.* 116 (2016) 195–201.
- [142] M. Wosniack, M. Santos, M. Pie, M. Marques, E. Raposo, G. Viswanathan, M. da Luz, Unveiling a mechanism for species decline in fragmented habitats: fragmentation induced reduction in encounter rates, *J. R. Soc. Interface* 11 (91) (2014) 20130887.
- [143] B.B. Niebuhr, M.E. Wosniack, M.C. Santos, E.P. Raposo, G.M. Viswanathan, M.G. Da Luz, M.R. Pie, Survival in patchy landscapes: the interplay between dispersal, habitat loss and fragmentation, *Sci. Rep.* 5 (2015) 11898.
- [144] T. Dannemann, D. Boyer, O. Miramontes, Lévy flight movements prevent extinctions and maximize population abundances in fragile Lotka–Volterra systems, *Proc. Natl. Acad. Sci.* 115 (15) (2018) 3794–3799.
- [145] W. Allee, E.S. Bowen, Studies in animal aggregations: mass protection against colloidal silver among goldfishes, *J. Exp. Zool.* 61 (2) (1932) 185–207.
- [146] Y. Gruntfest, R. Arditi, Y. Dombrovsky, A fragmented population in a varying environment, *J. Theoret. Biol.* 185 (4) (1997) 539–547.
- [147] R. Dorfman, A formula for the Gini coefficient, *Rev. Econ. Stat.* (1979) 146–149.
- [148] R. Bendel, S. Higgins, J. Teberg, D. Pyke, Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations, *Oecologia* 78 (3) (1989) 394–400.