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Optimal foraging strategies for mutually avoiding competitors

Farnaz Golnaraghi [a], David A. Quint [b], Ajay Gopinathan [a,*]

[a] Department of Physics, University of California - Merced, 5200 North Lake Road, Merced, 95343, CA, USA
[b] Physical and Life Sciences (PLS), Lawrence Livermore National Laboratory, 7000 East Avenue, Livermore, 94550, CA, USA

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ABSTRACT

Many animals are known to exhibit foraging patterns where the distances they travel in a given direction are drawn from a heavy-tailed Lévy distribution. Previous studies have shown that, under sparse and random resource conditions, solitary non-destructive (with regenerating resources) foragers perform a maximally efficient search with Lévy exponent μ equal to 2, while for destructive foragers, efficiency decreases with μ monotonically and there is no optimal μ. However, in nature, there also exist situations where multiple foragers, displaying avoidance behavior, interact with each other competitively. To understand the effects of such competition, we develop a stochastic agent-based simulation that models competitive foraging among mutually avoiding individuals by incorporating an avoidance zone, or territory, of a certain size around each forager which is not accessible for foraging by other competitors. For non-destructive foraging, our results show that with increasing size of the territory and number of agents the optimal Lévy exponent is still approximately 2 while the overall efficiency of the search decreases. At low values of the Lévy exponent, however, increasing territory size actually increases efficiency. For destructive foraging, we show that certain kinds of avoidance can lead to qualitatively different behavior from solitary foraging, such as the existence of an optimal search with $1 < \mu < 2$. Finally, we show that the variance among the efficiencies of the agents increases with increasing Lévy exponent for both solitary and competing foragers, suggesting that reducing variance might be a selective pressure for foragers adopting lower values of μ. Taken together, our results suggest that, for multiple foragers, mutual avoidance and efficiency variance among individuals can lead to optimal Lévy searches with exponents different from those for solitary foragers.

1. Introduction

Living organisms forage in order to find resources such as food or to reproduce by mating. An underlying motivation for their foraging movement is therefore to search for and increase their encounters with such resources. Optimal Foraging Theory (OFT) considers that animals aim to maximize a currency such as net caloric gain per unit time, subject to constraints that could be physiological or environmental. For fixed constraints, therefore, OFT would predict that organisms would adopt the most efficient search strategy (Viswanathan et al., 1999).

The search strategy can be guided by external cues such as visual, auditory or olfactory stimuli or even previous memories, which could help increase efficiency. However, when the locations of resources are not known *a priori* and there are no directional cues, a natural question that arises is whether organisms can optimize a completely stochastic search (Viswanathan et al., 2011).

In such a situation, in the case of sparse targets, many animals such as the albatross exhibit foraging patterns where distances traveled are drawn from a heavy tailed Lévy distribution, $P(l_j) \sim l_j^{-\mu}$, where $1 < \mu \leq 3$ (Viswanathan et al., 1996, 1999), with the direction of movement chosen from a uniformly distributed angle. When $\mu \leq 1$, the motion is ballistic and with $\mu > 3$, it reduces to Brownian motion, with a crossover between the two for intermediate values of μ. Similar foraging patterns, with $1 < \mu \leq 3$, was observed in a wide range of other organisms such as jackals (Atkinson et al., 2002), bacteria within a swarm (Ariel et al., 2015), T-cells (Harris et al., 2012), and spider monkeys (Ramos-Fernández et al., 2004). It has been shown theoretically that, in the case of sparse and randomly distributed targets that regenerate immediately after consumption (non-destructive foraging), the search efficiency, (η), is optimized around $\mu = 2$, where (η) is defined as the ratio of total number of targets found, to the total distance traveled (Viswanathan et al., 1999). This is consistent with the behavior of several foraging animals (Viswanathan et al., 1999), including the ones mentioned above, lending validity to the model.

Several extensions to this basic model have been studied to gain insights into more realistic foraging and they show the existence of different optimal strategies under different conditions.

* Corresponding author.
E-mail address: agopinathan@ucmerced.edu (A. Gopinathan).

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One example is when resources take a finite time to regenerate, as would be the case for plant-based food sources such as grass, flowers or fruits. For cases where the regeneration time far exceeds the foraging timescales, foraging is destructive and no optimal μ value is observed with efficiency decreasing monotonically as μ increases (Viswanathan et al., 1999, 2011, 2000, 2002) from 1. Tuning the regeneration time between the extremes of destructive and non-destructive can result in a crossover regime where the optimum strategy shifts in the range of μ between 1 and 2. (Santos et al., 2004).

Targets can also display various types of spatial distributions such as patchy, or normally distributed. For cases of low target density, when targets are non-regenerative and Lévy distributed with exponent close to 3, an optimal Lévy exponent for the searcher is observed around $\mu \approx 2$ (Ferreira et al., 2012), while for patchy distributions at high density, less super-diffusive strategies, ($2 < \mu < 3$), perform nearly as well as $\mu = 2$ (Wosniack et al., 2017). On the other hand, sparse but patchy distributions can result in tunable, highly super-diffusive, optimal search strategies with Lévy exponents in the range $1 < \mu < 2$ (Raposo et al., 2011). The topography of the environment can also have an effect on search efficiency. For example, when the environment has a concave porous topography (Volpe and Volpe, 2017), the search is optimized for destructive foraging (non-regenerative resources) around $\mu = 2.4$. Finally, an interplay between landscape size, number of targets and search termination can lead to an optimum that can be tuned over the entire range $1 < \mu < 3$ (Zhao et al., 2015).

While solitary foragers have been extensively studied, in many natural settings, multiple organisms cooperate or compete with each other for resources. Studies have shown that Brownian searchers with even rudimentary, purely repulsive interactions can minimize their mean first-passage time (MFPT) to targets with optimal, intermediate values of the interaction strength (Tani et al., 2014). Furthermore, search times are minimized for both Brownian and Lévy searchers when the range of cooperation is optimized, but Lévy strategies can be faster (Martínez-García et al., 2014). Along these lines, studies on the effects of communication on the foraging patterns of Mongolian gazelles showed that communication over intermediate length scales leads to a faster search and minimizes the MFPT to targets (Martínez-García et al., 2013). Cooperative foraging in hierarchical groups with a specific leader have also been found to benefit from Lévy strategies, though they may happen at the expense of group cohesion (Santos et al., 2009). Mixtures of strategies have also been shown to help cooperative foraging. For example, the search efficiency of a group of foragers, who can either search independently or by following others who find target patches, is maximized for a mixture of the two strategies. If searchers only follow other successful individuals, target patches might become depleted before they arrive at the site (Bhattacharya and Vicsek, 2014).

While such cooperative behaviors have evolved in many instances, competitive interactions between foragers for limited resources are also quite common. Mutual spatial avoidance is a generic behavior that has emerged in a variety of species, ranging from tigers (Carter et al., 2015) to rodents (Borremans et al., 2017), to ameliorate the negative consequences of competitor co-localization. These consequences include reduced gain from the same resources and potentially lethal encounters among aggressive individuals. Mutual avoidance can occur over a range of spatial and temporal scales and can be mediated by visual, acoustic, scent or other chemical cues. At one end of the spectrum are territorial predators that maintain territories over kilometers and years, mainly through scent marking. Lions (Heinsohn, 1997), tigers (Burger et al., 2008; Carter et al., 2015), wolves (Lewis and Murray, 1993), and mountain lions (Hornocker, 1969) establish and maintain static territories, or fixed exclusive areas, where there is an abundance of resources to survive and to reproduce. Furthermore, some animals such as red fox, dynamically modify their territories based on the trajectories of other animals as their scent marks start to disappear over time (Giuggioli et al., 2011). At the other end of the spectrum, mutual avoidance may be just restricted to the immediate proximity of an individual typically reinforced with direct sighting in animals that live in social collectives. For example, animals such as oystercatchers (Stillman et al., 1997), red knots (van Gils et al., 2015), swans (Gyimesi et al., 2010), and rodents (Borremans et al., 2017) avoid interfering with other cogeneric individuals in a close vicinity during the foraging process. Such contact avoidance interactions not only help minimize antagonistic encounters within the group but are also known to help facilitate collective motion in swarms and flocks (Couzin et al., 2002; Katz et al., 2011; Charlesworth and Turner, 2019). Interestingly, general, unifying models of animal interactions have been developed that can describe both foraging and collective motion (Potts et al., 2014).

While mutual avoidance is clearly a common behavior across a range of spatiotemporal scales, its' effects on foraging are less well studied. Here we develop and use a stochastic agent based model to understand how such mutual avoidance interactions can influence foraging efficiency as a function of foragers density, avoidance distance and intrinsic search strategy.

We explore different types of strategies that can optimize group foraging in these cases. In our simulations, each identical agent has an avoidance zone or territory with a fixed size, r_t, around itself which is not accessible by the other searchers. We study the effect on foraging efficiency of varying the territory size and the number of foragers. We do this with two different protocols. In the first protocol, we study "terrestrial" animals, who are not able to cross a competitor's territory, such that they are forced to stop at the intersection of the excluded region and their own path. In the second protocol, we study "aerial" animals. In this case, foragers are allowed to pass through or over others' territories, but they cannot forage in it. We note that our model assumes that foragers always know where the boundaries of a competitor's territory are either by direct visual contact with the competitor for small territories or by using scent markings or long range acoustic cues for large territories where the competitors may not be visible. We also note that for the case of very large territories, our model does not address the foraging process within the territory but rather the movement of the territory's center over much larger timescales as the animal forages for a new or more resource rich territory as is the case for transient male predators during dispersal as they seek to establish their independent territories (Carter et al., 2015). Using this model, we study the difference between the efficiency of a group of competitors and a single searcher performing Lévy flights of varying index μ. We look at varying the density of agents and size of their territory, r_t, and how it affects the search efficiency, and thus the search strategy of territorial competitors while performing Lévy flights. We also compute the variance in efficiency among multiple competing foragers as a function of the system parameters with a view to shedding light on optimizing searches in situations where minimizing variability is an important factor in addition to maximizing efficiency.

2. Model and simulation

Here we describe our agent-based model that we used to study foraging in a group of mutually avoiding competitors. Each individual agent performs a random walk consisting of a series of steps in random directions and has a perceptive range, r_v, within which it can detect resources. The step-lengths are drawn from a heavy-tailed Lévy distribution that is bounded:

$$p(l_j) = \frac{\mu - 1}{l_0^{1-\mu} - l_{max}^{1-\mu}} \left(l_j\right)^{-\mu} \tag{1}$$

The Lévy exponent is within the range of $\mu \in (1, 3]$. The smallest step-length we allow the forager to take is $l_0 = r_v$ because steps smaller than the vision radius, r_v, will not be beneficial. The maximum step-length, l_{max}, is equal to L, the size of our system. This is due to the fact that steps larger than the size of a landscape, L, are not realistic and unbounded displacements, or infinite step-lengths, are naturally

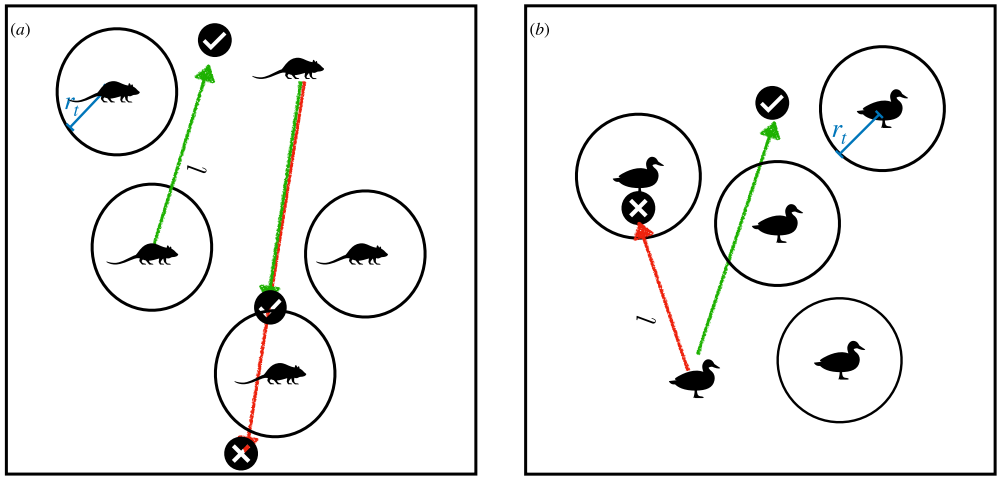

Fig. 1. Schematic illustration of foraging protocols. (a) Terrestrial animals are not allowed to cross other foragers' territories. (b) Aerial animals are allowed to cross other foragers' territories, but cannot land in it.

forbidden (Wosniack et al., 2017). The mean free path between two successive targets is defined as:

$$\lambda = (2r_v\rho)^{-1}, \tag{2}$$

where ρ is the target density (total number of targets over total area). The efficiency of the search, (η), is the ratio of total target found (N_{total}) over total distance traveled (L_{total}), or the inverse of average flight length $\langle l \rangle$ times the average number of flights (N) between two successive targets:

$$\eta = \frac{N_{total}}{L_{total}} = \frac{1}{\langle l \rangle N} \tag{3}$$

The Lévy flight foraging procedure for a single agent with targets works as follows Viswanathan et al. (1999):

1. At each time step, if there are multiple targets within the foragers perceptive range, r_v, the agent goes to the nearest target.
2. If there are no targets nearby, the forager picks a random flight length, l_j, from the Lévy distribution (Eq.(1)), and a random uniformly distributed angle between 0 to 2π, and starts the next flight.
3. The forager is constantly looking for targets within its vision radius, r_v, while it is taking the steps along its way.
4. If a target site is within r_v, the forager goes to it. Otherwise, it completes that flight path, l_j, and repeats steps 1 and 2.

For a solitary forager, the average number of flights between two successive targets, N, depends on whether the search is destructive or non-destructive (non-regenerative or regenerative resources). For destructive searches, $N_d \approx (\frac{\lambda}{r_v})^{\mu-1}$, and $N_n \approx (\frac{\lambda}{r_v})^{\frac{\mu-1}{2}}$ for non-destructive searches (Viswanathan et al., 1999; Buldyrev et al., 2001). For a solitary agent, the efficiency is maximized as a function of Lévy index μ, with value $\mu = 2$, (Viswanathan et al., 1999).

To model multi-agent foraging we consider N_f foragers which are randomly placed in a two dimensional box of size L with periodic boundary conditions. The periodicity is applied to the movement of the foragers, as well as the regeneration of the targets. Targets are distributed randomly, from $[0, L]$ in x and y, and, in the non-destructive case, they are regenerative such that at each time step, we have a fixed number of targets. Each forager has a territory with radius r_t around itself which is not accessible by the other foragers. Individual foragers perform flights according to the Lévy flight foraging procedure specified above with modifications due to interactions detailed below. At each step, foragers perform their flights in a random order to avoid bias. We define two different protocols for our foragers to model terrestrial and aerial animals. In our first protocol, terrestrial, foragers are not able to cross another forager's territory, and they are forced to stop at the intersection of the excluded region and their path. In our second protocol, aerial, foragers are allowed to cross other foragers' excluded region but they cannot forage in it. The foraging pattern, for the first protocol (Fig. 1a), terrestrial, is then as follows:

1. At each step, a random order of foragers is chosen. When one forager finishes the following steps, the next forager starts. By the end of the step, all agents have performed one flight.
2. The chosen forager picks a random flight length, l_j, from the Lévy distribution (Eq.(1)), and a uniformly distributed random angle.
3. The forager starts moving, and uses Lévy flight foraging procedure to find targets (Viswanathan et al., 1999).
4. If the forager's path intersects with other territories, the forager stops at the intersection of its path and the excluded region.
5. If a target is inside of the other foragers territory, the forager will skip that target, to remain consistent with the given protocol.
6. Steps 1 to 5 are repeated until the maximum number of steps of the simulation is reached.

The foraging pattern for the second protocol (Fig. 1b), aerial, is similar to the terrestrial protocol, except for step (4). In this case, if the end point of the forager's flight is inside of another forager's excluded region, step (2) needs to be repeated. We note that the first protocol is meant to represent terrestrial animals because they can sense competitor territories and we assume that they stop the moment that they hit the periphery of an excluded region. Similarly, the second protocol represents aerial animals, since the agents are able to see the end point of their flight at the beginning, and choose another random path to avoid landing inside a competitor's territory. It can also model terrestrial animals with a visual range for competitors that is much larger than the territory size, allowing the animal to choose a path that avoids stopping in the competitor territory.

3. Results

The interaction between the foragers affects the search efficiency, and potentially changes the optimal foraging strategy by changing the encounter rate. Two factors influence this rate, the number of foragers, N_f, and radius of their territory, r_t. By increasing the number of foragers, as well as the radius of the territory, the encounter rate between foragers will increase. In what follows, we study cases with two, four and eight agents with territory radius $10 < r_t < 100$. Unless otherwise stated, the simulation box size, number of targets and vision radius are fixed as $L = 500$, $N_{targets} = 25$, $r_v = 1$.

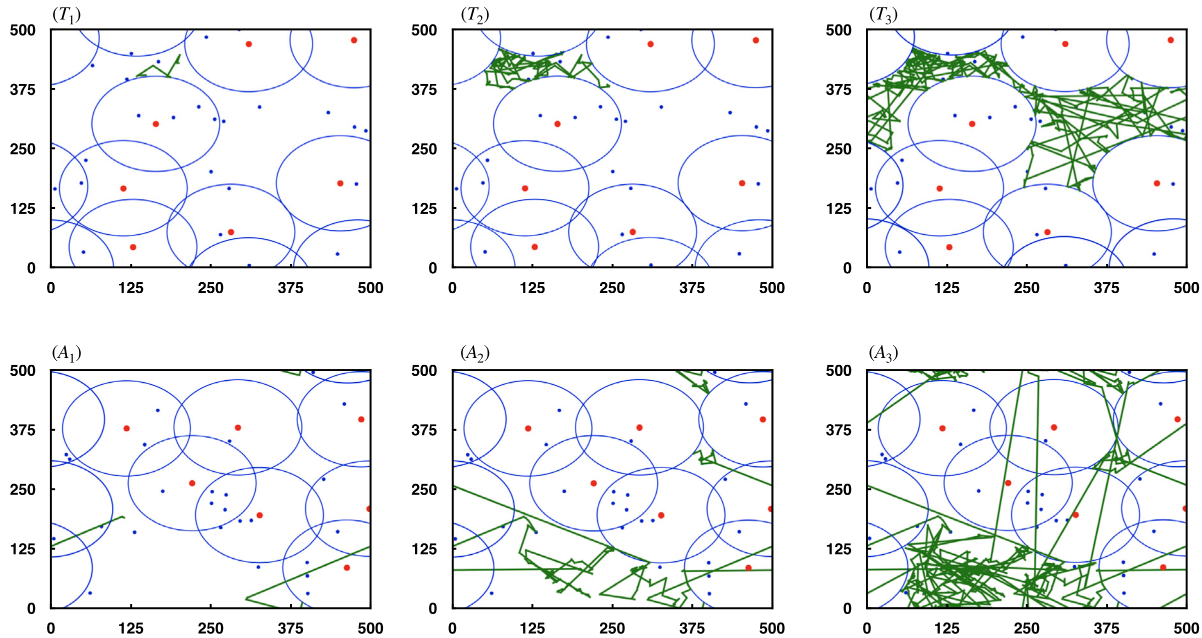

Fig. 2. In the top row, T_{1-3}, are snapshots of simulations (after 10, 150 and 500 flights respectively) for the terrestrial case, with $N_f = 8$ and $r_t = 100$, where the green path represents the foraging pattern for 1 forager. The bottom row, A_{1-3}, shows snapshots of simulations (after 10, 150 and 500 flights respectively) for the aerial case, with $N_f = 8$ and $r_t = 100$. $\mu = 2$ in both cases. For visualization purposes, the other 7 agents are stationary in this set of simulations.

In the terrestrial case (Fig. 2T_{1-3}), we notice that increasing the radius of territory, r_t, and the number of agents, N_f, leads to lower efficiencies (Fig. 3) overall. However, the optimal Lévy index μ is still approximately equal to 2 (Fig. 3a,b). To investigate this further, we look at the inverse of average number of flights ($\frac{1}{N}$) and the inverse of average flight length ($\frac{1}{\langle l \rangle}$) as a function of radius of territory, r_t, for different values of μ since the efficiency is defined as $\eta = \frac{N_{total}}{L_{total}} = \frac{1}{\langle l \rangle N}$. We observe that steps become truncated, so that the inverse average step length increases as a function of r_t (Fig. 3c). At the same time, fewer targets are accessible to each forager because they are enclosed by other agents' territories. Therefore, the inverse of number of steps between two successive targets decreases as a function of r_t for different values of μ (Fig. 3c inset). The relative reduction in the number of targets found is however larger than the reduction in the distance traveled (Fig. 3d) leading to net decrease in efficiency with increasing r_t for μ greater than about 1.4. However, counter-intuitively, we note that the efficiency is *higher* for larger r_t and larger number of foragers when μ is smaller than 1.4 (Fig. 3a,b). The reason for this is that, for small μ and small r_t values, very long jumps are more likely to occur. So, the agents end up taking long jumps without finding as many targets. Therefore, the natural truncation in the step-lengths for larger r_t values is in fact beneficial for the agents and it prevents them from traveling long distances without finding resources. This is also reflected in the fact that the relative reduction in the number of targets found is *smaller* than the reduction in the distance traveled for $\mu < 1.4$ (Fig. 3d). Thus, territorial competition can be beneficial in the limit of low μ, de-localized search strategies.

When we compare the aerial (Fig. 2A_{1-3}) and the terrestrial (Fig. 2T_{1-3}) cases, we notice that, as for the terrestrial case, the efficiency in the aerial case decreases when the number of foragers, and radii of territory increases (Fig. 4a,b). We also observe a lower efficiency for the aerial case compared to the terrestrial case that is more pronounced for lower values of μ. The average flight length in the terrestrial case is lower than the aerial case, since in the aerial case, agents are still allowed to take longer jumps. Since the steps still come from the same Lévy distribution, bigger flight lengths can occur (Fig. 4c). However, in the terrestrial case, $\langle l \rangle$ decreases by increasing r_t because foragers are forced to stop if their path intersects with other territories. The total number of targets found in both cases decreases by increasing r_t, since targets in other foragers territories, are not accessible to all of the foragers. However, the number of targets found does not significantly increase with decreasing μ, compared to the terrestrial case which is shown in (Fig. 4c inset). This can also be seen in the ratio of total targets found in the aerial case to the terrestrial case as well as the ratio of the average flight lengths in the two cases, plotted as a function of μ in (Fig. 4d). We see immediately that the average flight length, $\langle l \rangle$, ratio is significantly higher than the ratio of targets of found N_{total} for smaller values of μ (Fig. 4d). This results in a greater suppression of the efficiency in the aerial case for small values of μ.

While we have so far considered the mean efficiency of the population, we now consider a measure of the variance by computing the standard deviation of the efficiencies among agents. We also look at this standard deviation for many solitary foragers with different starting points. We consistently observe a higher standard deviation for higher μ values even after traveling long distances (Fig. 5a), and the deviations are of comparable magnitude for the terrestrial, aerial and solitary searchers. Therefore, there is no significant difference between territorial searchers and solitary searchers in terms of the variance of the efficiency among foragers. We note that, though the standard deviation will eventually vanish after long enough times, it is important to consider variance among individuals at intermediate times that could be of biological relevance, such as seasons or reproductive intervals. This standard deviation, in fact, increases monotonically as μ increases in all cases (Fig. 5b). This indicates that foraging strategies with higher μ values, or shorter step lengths may lead either to a highly efficient search or a search with an efficiency well below the average efficiency of the population. For a search with smaller Lévy index and larger flight lengths, on the other hand, the variance is small, and all the agents perform a search with efficiency close to the average. We can rationalize this by considering that at higher μ values, due to the smaller step sizes, less space is sampled within a certain time, and so if an agent is in part of a space which has more (or less) resources, it will have a more (or less) efficient search. For smaller μ values, longer flights are dominant, and chances of visiting different spots of the landscape within the relevant time will be higher. Therefore, the

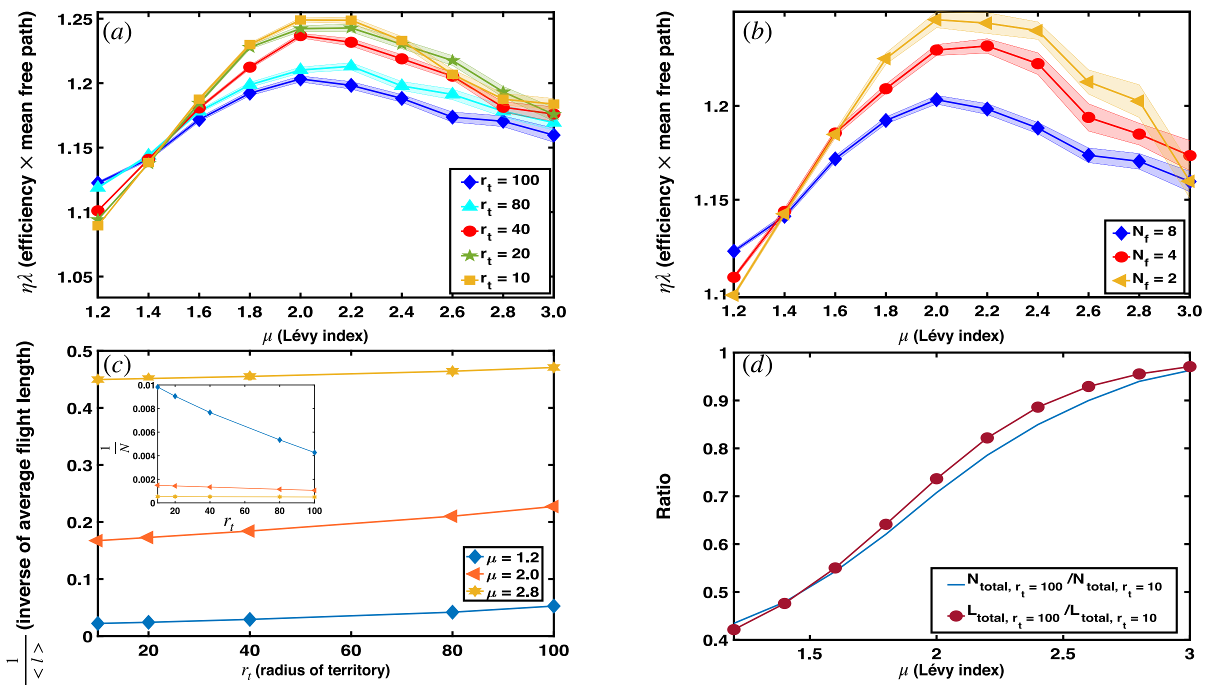

Fig. 3. (a) Efficiency η versus μ for eight agents ($N_f = 8$), and different radii of territory ($r_t = 10, 20, 40, 80, 100$). (b) Efficiency η versus μ for $r_t = 100$ and different number of agents ($N_f = 2, 4, 8$). The spread is the standard error of the mean and the solid lines are the average efficiencies. (c) Inverse of average flight lengths, $\frac{1}{\langle l \rangle}$, as a function of r_t. Inset is the inverse of the average number of flights between two successive targets, $\frac{1}{N}$. Both plots are for different values of Lévy index $\mu = 1.2, 2.0, 2.8$. (d) Ratio of total targets found (blue) and total distance traveled (red) for $r_t = 100$ and $r_t = 10$. $N_f = 8$ in (c) and (d).

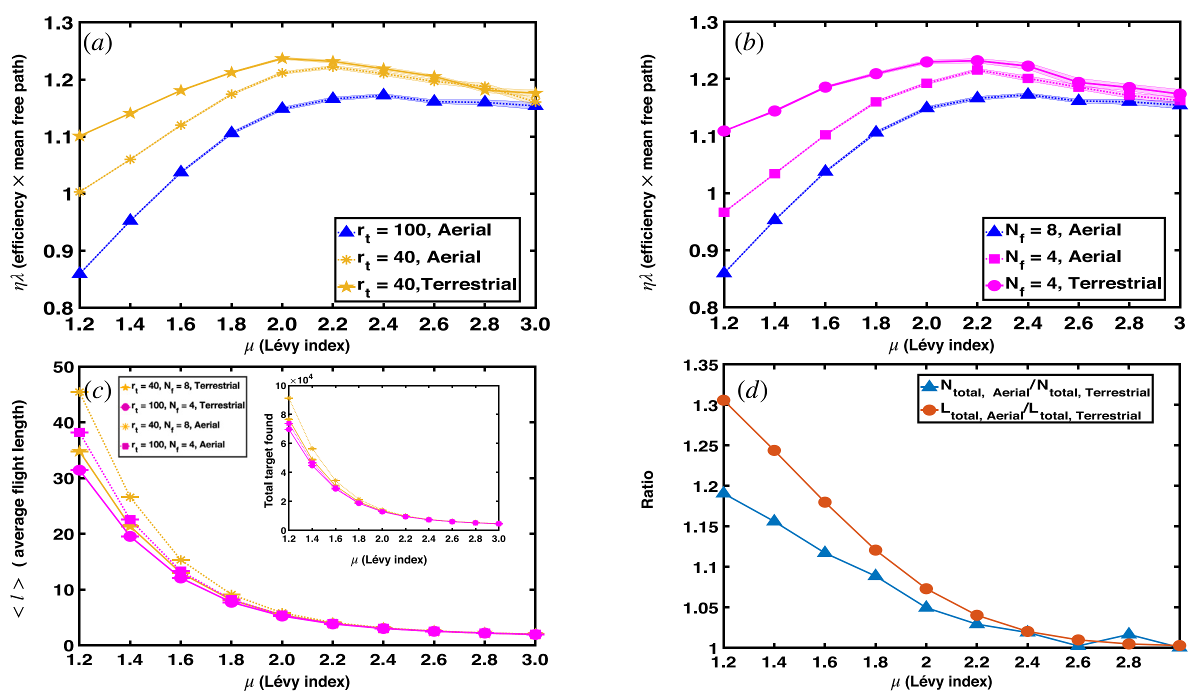

Fig. 4. (a) Efficiency for the aerial case ($r_t = 40{,}100$) and the terrestrial case ($r_t = 40$) for $N_f = 8$. (b) Efficiency for the aerial case ($N_f = 4, 8$) and the terrestrial case ($N_f = 4$) for $r_t = 100$. (c) Average flight length for the terrestrial (solid lines) and aerial (dashed lines) case. Inset is total target found for the terrestrial(solid lines) and aerial(dashed lines) case. (d) Ratio of total targets found (blue) and total distance traveled (red) between the aerial and the terrestrial cases for $r_t = 40$ and $N_f = 8$.

searcher is able to better sample the entire space, resulting in a smaller variance.

Finally, we look at the efficiency in the destructive case, where targets will not be able to grow back after they are found. In the terrestrial case, the behavior is similar to a single searcher (Viswanathan et al., 2011) with no optimal value for μ (Fig. 6a), and the efficiency decreasing as μ increases. We also see that increasing territories results in slightly suppressed efficiencies. In the aerial case, however, we see a peak in the efficiency as a function of μ especially for higher r_t, indicating the existence of an optimal strategy for destructive foraging in this case. This peak arises from the same effect in the non-destructive aerial search where the efficiency is suppressed for smaller μ values and

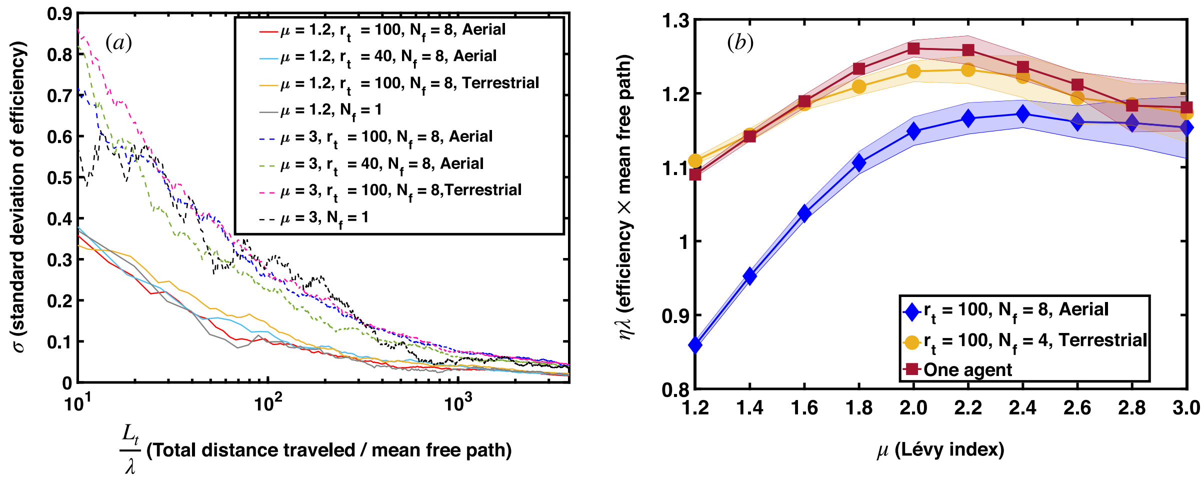

Fig. 5. (a) The standard deviation of the efficiency over distance traveled for the terrestrial, aerial and single forager cases. (b) Efficiency as a function of μ for the aerial, terrestrial and single forager cases. The shaded region around the mean efficiency is the standard deviation measured after $N = 10^7$ flights.

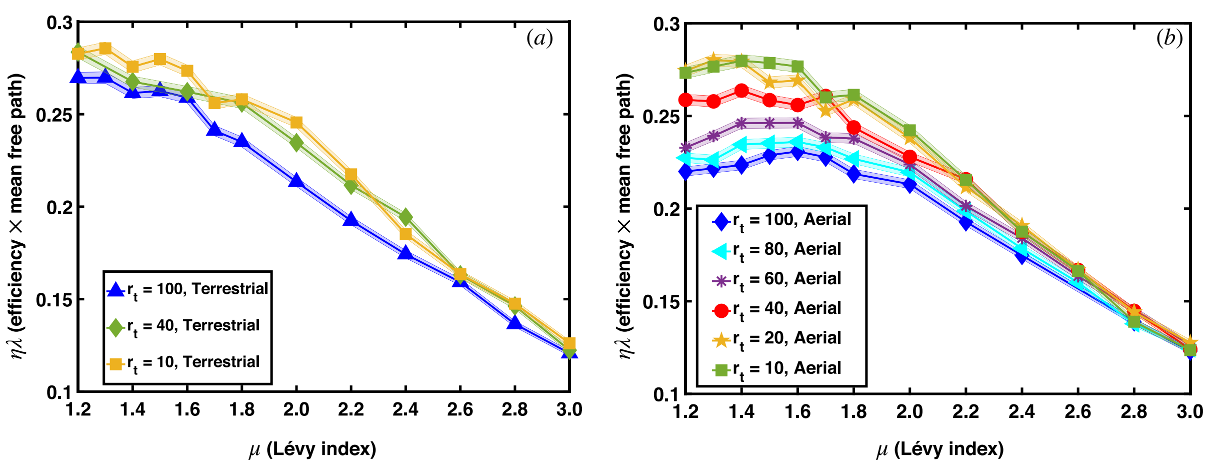

Fig. 6. Non-regenerative search efficiency as a function of μ. The spread is the standard error of the mean and the solid lines are the average efficiencies. (a) For the terrestrial case, we observe no optimal Lévy index μ and the behavior is similar to a single forager. (b) For the aerial case, we observe a tunable optimum in efficiency as r_t increases. $N_f = 8$ in (a) and (b).

higher r_t, since longer jumps are allowed, but agents cannot access the targets (Fig. 6b). In this case, this suppression creates a slight peak in the efficiency around $\mu = 1.6$ for higher r_t values (Fig. 6b). We note that the optimum shifts to the left and becomes less pronounced for smaller r_t indicating an optimum that is tunable by territory size.

4. Summary and discussion

It has been established that many solitary foragers such as goats (De Knegt et al., 2007), spider monkeys (Ramos-Fernández et al., 2004), and even single cells (Harris et al., 2012) perform Lévy flight type search patterns while looking for sparse, randomly located resources. While the actual statistics of the searches are debated and myriad factors including memory, topography, spatial and temporal distribution of resources can affect the optimal strategy (Reynolds and Bartumeus, 2009; James et al., 2011; Yoda et al., 2012), it is clear that searches do contain steps from long-tailed distributions and optimization principles are at work. The analysis of simple, minimal models have provided rigorous, quantitative frameworks to analyze such behavioral patterns and uncover potential reasons for observed strategies.

In this spirit, to understand the effects of avoidance interactions on foraging strategy, we have introduced a minimal model of group foraging with territorial competition.

For a single searcher looking for regenerating resources, the efficiency of search is maximized when a combination of localized and non-localized steps are taken. In the case of sparse targets, the most beneficial search strategies observed are Lévy flights with $\mu \approx 2$ (Viswanathan et al., 1999). We showed that, in the presence of competition, strategies maximizing the efficiency are similar to those for single searchers and the optimal Lévy exponent, μ, is still approximately 2. However, in both terrestrial and aerial cases, the efficiency of the search generally decreases when the number of agents and the size of territory increases, i.e. increasing competition leads to lower overall efficiency for the group. However, for μ values close to 1, in the terrestrial case, larger territories, limiting the motion of foragers, are beneficial and increase the search efficiency because they cause a truncation in foragers step lengths. This truncation prevents foragers from traveling long distances without finding targets. Thus an increase in territorial competition can increase the efficiency of the group.

For destructive foraging, where targets do not regenerate after being consumed, the optimal search strategy for solitary foragers within the minimal model is purely ballistic. This can change when targets are distributed in patches or can occasionally evade capture or the landscape is porous and concave (Reynolds and Bartumeus, 2009; Ferreira et al., 2012; Volpe and Volpe, 2017). Here, we show that, for terrestrial foragers, similar to solitary foragers, the optimal strategy is still ballistic and the efficiency decreases as the size of territory or population of foragers increase. However, for the aerial foraging case, where long jumps are allowed, and resources are limited, an optimum appears. For long-ranged searches, large territories limit the access to the targets by other foragers, and since crossing is allowed, agents end up taking very long jumps without finding any targets. This results in a suppression in the efficiency for small μ values and creates an optimum that depends on the territory size. The optimum eventually disappears for small territories since the targets become more accessible and the optimal strategy becomes ballistic.

Finally, in addition to looking at the mean efficiency of the group, we also focused on the variance in efficiencies among individuals which is potentially of biological significance in contexts where bounding the lowest efficiencies in a group might be important. We found that the variance among the efficiencies of individual foragers in a group was similar to the variance in the efficiencies of many solitary foragers. For small Lévy exponent, μ, values the variance is small, and for large μ values the variance increases. This suggests that, if minimizing variance is a selective pressure (to lower the chances of starvation for example), then a strategy with a lower μ than is optimal to maximize the mean may be manifested. In particular, for non-destructive foraging, this could lead to individuals and groups exhibiting Lévy strategies with $\mu < 2$. Interestingly such long-ranged searches may be more advantageous for territorial competitors than solitary foragers as their mean efficiency is also higher in this regime.

It is to be noted that we chose to model the search strategies of individuals who are in the presence of competitors by Lévy flights. This choice was motivated by several reasons. It is the simplest model for uninformed searches that covers the spectrum from Brownian to ballistic searches by tuning a single parameter. There is also evidence that patterns giving rise to Lévy searches might be intrinsically generated by neural networks (Sims et al., 2019) in which case it is a natural base model that may be adaptively modified. It is also conceivable that individual Lévy search strategies evolved first with fine-tuning coming later to deal with competition. Finally, many of species that we consider such as deer and monkeys (Ramos-Fernández et al., 2004; Focardi et al., 2009) switch between individual and group exploration, making a Lévy search a natural base behavior.

We now discuss specific examples of situations where our results may apply. Studies which include comparisons of individual and group behavior are particularly relevant and include analyses of fallow deer (Focardi et al., 2009) and spider monkey foraging (Ramos-Fernández et al., 2004). Interestingly, while individual deer were found to forage with a $\mu \approx 2$, consistent with the optimal foraging prediction for sparse, regenerating resources (here grass), individual monkeys performed searches for fruiting trees with $\mu \approx 1.5$. One possibility is that the clearly finite regeneration time for fruit could result in a shift toward more destructive type foraging and hence a shift in optimal strategy toward ballistic searches (Santos et al., 2004). In this case, though, one might expect much more ballistic searches given the vast disparity in regeneration time (year) and the foraging time (hours) making it almost fully destructive. Another intriguing possibility is that minimizing variance may be important for individual monkeys, which, our work shows, leads to more ballistic searches as well. In both spider-monkeys and deer, it was apparent that groups exhibited shorter ranged search patterns (either with a higher μ or exponential) than individuals, which could be due to the effects of group cohesion disfavoring long range excursions. In the case of spider-monkeys, the observed μ when individuals were part of a group was indeed close to 2, indicating, perhaps that minimizing variance is not important when part of the group. There was also no evidence of notable 'terrestrial' exclusion in these two cases (based on overlapping trajectories), indicating either very short ranged mutual avoidance, if any, or 'aerial' mutual avoidance allowing individuals to pass by, but not forage, within a certain excluded zone. To really pin down any avoidance requires simultaneous tracking of multiple foragers in groups and computing correlations between their locations. This would be an interesting direction for future field studies.

It is interesting to note that many animals display foraging strategies with μ that are below 2. These include Magellanic penguins foraging with a Lévy exponent of $\mu = 1.7$ (Sims et al., 2008), Blue sharks with $< 1.6 < \mu < 2.3$ (Humphries et al., 2010), sub-populations of grey seals (Austin et al., 2004) with $1.1 < \mu < 1.3$, black-browed and wandering albatrosses with 1.27 and 1.19 respectively (Humphries et al., 2012), and jellyfish with μ as low as 1.18 (Hays et al., 2012). While finite regeneration times, landscape size and heterogeneity and termination can all be factors in these shifts (Santos et al., 2004; Raposo et al., 2011; Zhao et al., 2015), our work suggests that minimizing variance could be another factor to consider. Furthermore, in some of these cases, such as the grey seals, albatrosses and jellyfish, the μ is so low that groups of them could potentially boost their efficiency appreciably by displaying "terrestrial" avoidance. It would be fruitful to look for signatures of such behavior in field data.

Animals involved in destructive foraging can also display shifts from the ideal optimal ballistic $\mu \approx 1$ behavior. For example, groups of black-tailed gulls display $\mu \sim 1.5$ in human-caused foraging trips where the location of finite food resources is more predictable compared to natural foraging trips (Yoda et al., 2012) while elephant herds engage in destructive foraging (Shannon et al., 2006), with $1.8 < \mu < 2.4$ (Dai et al., 2007). Again, while factors such as target distributions, target mobility and landscape structure (Reynolds and Bartumeus, 2009; Ferreira et al., 2012; Volpe and Volpe, 2017) can contribute to these shifts, our work indicates that "aerial" avoidance could be another factor that could contribute to such deviations.

Finally, we note that the patchiness of resources can lead not only to different optimal strategies (Reynolds and Bartumeus, 2009) but also to long-term effects in species decline due to fragmentation of habitats and reduction in encounter rates (Wosniack et al., 2013; Niebuhr et al., 2015). It is interesting to consider how territorial mutual avoidance that we have studied here might exacerbate such long-term effects.

Overall, our work has shown that territorial competition can lead to the improved efficiency of very long-ranged searches and highlighted factors that can shift the optimum strategy of foragers including selective pressure on minimizing the variance of the efficiency favoring lower μ or more long-ranged strategies, and aerial territorial competition leading to the existence of shorter-ranged optimal strategies for destructive foraging. We hope that our results will help future work consider these additional factors quantitatively when analyzing foraging data from the field that show deviations from the simplest optimal strategies.

CRediT authorship contribution statement

Farnaz Golnaraghi: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing. **David A. Quint:** Conceptualization, Methodology, Software, Formal analysis, Writing, Supervision. **Ajay Gopinathan:** Conceptualization, Methodology, Formal analysis, Writing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

None.

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