To join or not to join: collective foraging strategies

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Abstract. We present a minimal model to address the issue of how the interaction between foragers influence their encounter rates with resources. We consider a two-dimensional lattice model to study the optimal strategy for a group of foragers (walkers) searching for targets distributed heterogeneously. A forager who has not detected any target has the choice of either joining other foragers in the neighbourhood, who have detected targets, or continue searching independently. The optimal strategy appears to be a mixture of these choices. Remarkably, we observe that scale-free walks appear for strategies far from optimality. In general, we investigate the behaviour of the model with a parameter characterizing the propensity of the foragers to aggregate and the radius of interaction characterizing the neighbourhood of a forager.

1. Introduction

The phenomena of foraging or searching is ubiquitous in nature. Animals are found to forage for food or shelter. The efficiency with which an individual animal can forage becomes a key to its survival. Conventionally, the subject of behavioural ecology has tried to understand, how the foraging behaviour determines the foraging efficiency in different species [1, 2]. However, the problem has been found to be relevant in several other contexts ranging from military search procedures [3], to proteins searching for target sites on the DNA [4]. Interestingly, theoretical investigations based on ideas in statistical physics have provided a paradigm for the analysis of the complexity of the phenomena [5, 6]. The frameworks of random walks and diffusion equations have been extensively used for modelling [7, 8]. The possibility of recording trajectories of animals searching for food have further facilitated such studies [9, 10].

To model the scale-free walk-length distributions of animals that forage alone, Lévy walks have been proposed [11, 12, 13]. Studies have shown that under certain conditions Lévy walks are optimal, but deviations greatly reduce the advantage of Lévy walks in favour of ballistic or Brownian motion [12, 14, 15, 16]. For a single animal looking for resources, the foraging efficiency is dependent on its searching strategy and the distribution of the targets [8, 11]. However, when in a group, the interactions between the foragers become important in determining the success rate. An animal which is unsuccessful in locating food by searching on its own, is usually found to locate other distant members who are successful and join them [1, 17, 18]. When food is abundant there is hardly any benefit for individuals to join others to increase the chance of encountering food. However, when the distribution of food in space is heterogeneous, or a temporal variation is present, interactions between the foragers may become important.

Several field studies and theoretical models have investigated how collective effects influence the search behaviour [19, 20]. For example, a stochastic environment was shown to initiate
cooperation between foragers [21]. Social behaviour in primates has been shown to give rise to scale-free move lengths [22]. Very recently, the influence of communication on the foraging pattern of gazelles was investigated [23]. The study showed that communication over intermediate length scales result in faster searches. Remarkably, the movement of gazelles was found to be Brownian.

In this paper we study the problem of collective foraging. In a recent investigation [24], we developed a minimal model to investigate the effect of interactions on the search efficiency, and the spatio-temporal scalings that emerged in the movement of foragers. In [24] we assumed a forager to be informed about the state of all other foragers at any instant of time. In the present investigation we assume a finite interaction radius for the foragers. In our model, the foragers are walkers on a lattice and a forager executes a random walk when it is independently searching for targets. We characterize the propensity of a forager to approach the nearest site where targets have been discovered, through a parameter. Unlike the foragers, the targets are immobile but regenerative. We study the resulting forager-target interactions by varying this parameter and the radius.

2. The model

Below, we provide a brief description of the model. We consider a two dimensional square lattice of size $L$ with the periodic boundary condition (PBC). The PBC is applied with regard to the movement of the foragers as well as the regeneration of the targets. There are $N_F$ foragers which are initially distributed randomly on this lattice. The targets are regenerative such that at every time step the total number is $N_T$. We define the neighbourhood of a forager as a circular region of radius $R$ centred on it. We assume that at any instant of time, a forager is able to determine its neighbours that have been successful in identifying and consuming food. However, a forager is only able to detect targets at the site where it has arrived. A forager which is searching for targets moves towards the nearest site in the neighbourhood, where, targets have been discovered, with probability, $p = \exp(-\alpha d)$, where $d$ is the distance to the site ($d < R$), or, continues executing a random walk (RW), with probability $1 - p$. We term the movement in the former case as a targeted walk (TW). A forager which is already executing a TW continues with it, unless the targeted site becomes empty of targets. In the latter case the forager reverts back to executing a RW. In the limit $\alpha \to \infty$, the foragers are not following each other and the trajectories of are essentially RWs. The tendency of foragers to travel towards distant sites, increases with decrease in $\alpha$. In general, the trajectories are a mixture of RWs and TWs. The detailed rules pertaining to the behaviour of foragers can be found in [24].

The rule pertaining to the regeneration of targets at every instant is as follows. Let $\Delta N(t)$ be the number of targets that have been consumed at any instant of time $t$. We randomly select one of the remaining $N_T - \Delta N(t)$ targets. At a distance $d$ ($1 \leq d \leq L/\sqrt{2}$) from the location of this target a new target is placed, in a random direction. The distance $d$ is chosen from a distribution $P(d) \sim d^{-\gamma}$, where $\gamma$ is a parameter. This process is repeated another $\Delta N(t) - 1$ times. Thus, the total number of targets at the beginning of the time step $t + 1$, again becomes equal to $N_T$. The distribution $P(d)$ generates targets distributed in well separated clusters with the parameter $\gamma$ effectively characterizing the degree of heterogeneity of the distribution. The method effectively creates a foraging environment with a high degree of spatio-temporal heterogeneity [21, 25, 26], and allows to preserve the overall statistical nature of the environment during the time evolution of the model. We also take, $N_F = N_T = N$, which would correspond to the case of targets being rather scarce, and we expect that collective effects are relevant when there is a scarcity of targets.
3. Results

We associate a radius \((r_0)\) with the area per particle, so that \(r_0 = L/\sqrt{N\pi}\). We choose to measure \(R\) in units of \(r_0\) such that \(R = m.r_0\), where, \(m\) is a positive integer. Having \(m < (L/r_0)\) implies that at any instant, on the average, a forager remains informed about the state of \(n < N\) other foragers with \(n < N\). In [24] we found that, \(n \sim m^\nu\), where, \(\nu = 2.23\). The Fig. 1(a) shows a typical snapshot during the time evolution of the model for \(N = 128, L = 128, \gamma = 2.5, \alpha = 0.0\) and \(n = N\). The position of the foragers is shown with different symbols. The figure reveals the spatial clustering of the targets. The snapshot corresponds to a case when the foragers are increasingly aggregating in a region where the density of the targets is high. This event also becomes apparent by looking at the trajectory of a typical forager. The trajectory is a mixture of RWs (marked in grey) and TWs (marked in black). However, the dynamics depicted in the figure is actually deterministic owing to the fact that \(\alpha\) is zero. A forager, searching for targets, is always drawn towards the nearest site where targets have been discovered, independent of the distance of separation.

For the rest of the study we take, \(N = 512, L = 512\) and \(\gamma = 2.5\). We define the efficiency of foraging, \(\eta\) as the ratio of the total number of targets consumed by all the \(N\) foragers, to the total distance travelled by all the foragers, in a given amount of time. We first allow the system to reach a stationary state and we collect the statistics over a period of \(10^6\) time steps starting from 200 arbitrary initial conditions. In Fig. 1(b) we plot \(\eta\) as function of \(\alpha\) for different values of \(m\). We note that the distance dependence of the decision to approach other foragers actually results from the span of the neighbourhood as well as the value of \(\alpha\). When \(\alpha \to \infty\) the foragers search independently through RWs, the collective effects are absent and the efficiency is the same for all values of \(m\). The efficiency is found to increase when \(\alpha\) is lowered. When targets are clustered in space, we expect that a forager travelling to a region where targets have already been discovered increases its own chance of encountering a target. For very small values of \(m\), the initial rise in efficiency is rapid. The parameter \(\alpha\) being the inverse of a length scale, for a given \(R\), we expect the rapid rise in \(\eta\) to occur when \(\alpha \sim 1/R\). For lower values of \(\alpha\), the

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**Figure 1.** (a) A typical snapshot during the time evolution of the model for \(N = 128, L = 128, \gamma = 2.5\) and \(\alpha = 0.0\). The foragers are shown with circles (blue) and targets are shown with squares (green). The path of a randomly chosen forager is drawn. The grey steps belong to random walks and the black steps belong to targeted walks. (b) Variation of the efficiency, \(\eta\), with \(\alpha\) for \(L = 512, N = 512\) and \(\gamma = 2.5\). The different symbols pertain to different values of \(m\) (and hence, \(R\)) and are shown in the legend.
increase is slow. This is because a forager does not detect other foragers at distances larger than $R$. Therefore, when the neighbourhood is small, following other successful foragers is always beneficial. For larger values of $m$, a maximum is seen to appear in $\eta$. This corresponds to the most efficient strategy in terms of $\alpha$. This strategy pertains to joining others when clusters are discovered nearby and opting to search independently, otherwise. Lesser values of $\alpha$ makes the foragers follow other foragers indiscriminately. When a cluster is discovered, a large fraction of the foragers are drawn towards it through TWs. This delays the discovery of other clusters in space. As a result the efficiency drops. We call the inverse of the optimal $\alpha$ as $d_{opt}$. In [24] we showed that, $d_{opt} \sim 1/N^\zeta$, for a given $L$, with $\zeta = 0.65$. Additionally, as $m$ increases further, the efficiency in $\alpha \rightarrow 0$ limit is found to become lesser than the $\alpha \rightarrow \infty$ limit. This crossover is seen to occur at around $m = 4 = m_c$, which suggests $m_c r_0 \sim d_{opt}$.

The TWs are signature of the collective effects and we measured the fraction of walkers ($f_t$) that execute TWs at any instant (Fig. 2)(a). In general, for a given value of $m$, when $\alpha$ is decreased, we find $f_t$ to increase rapidly at the beginning and then slowly, later. The reason is very similar to what was discussed in the previous paragraph. Lowering of $\alpha$ causes foragers to follow neighbours through TWs but because of the finite size of the neighbourhood the increase in $f_t$ is slowed down. However, for a given $\alpha$, $f_t$ is found to increase with $m$. This is because the larger the neighbourhood, the greater is the chance that a forager detects another successful forager. However, in the extreme case when $R$ encompasses the whole of the lattice ($n = N$), we find there is a maximum in $f_t$. This is related to the drop in efficiency, $\eta$. In this particular case, when $\alpha \rightarrow 0$, all the foragers get involved in TWs on the discovery of a cluster, the simultaneous discovery of a new cluster is prevented, and as such less number of TWs take place on the average at any instant.

We found that on the simultaneous discovery of clusters foragers execute TWs from one cluster to another. To characterize this collective movement we used the flocking order parameter [27], modified for the lattice, $\Phi = \sqrt{(f_{x+} - f_{x-})^2 + (f_{y+} - f_{y-})^2}$, where $f_{x+}$ denotes the fraction of foragers moving towards the positive $x$-direction at any instant, and likewise. A large value of $\Phi$ would imply that, on the average, the foragers are moving in the same direction, at any instant of time. In Fig. 2(b) the plot $\Phi$ versus $\alpha$ is shown. The dependence of $\Phi$ on $\alpha$ is

Figure 2. Plots of the fraction of walkers executing targeted walks at any instant, $f_t$ (a) and the flocking order parameter, $\Phi$ (b) against $\alpha$ for $L = 512$, $N = 512$ and $\gamma = 2.5$. The different symbols correspond to different values of $m$ and are the same as that in the Fig. 1(b).
very similar to that of $\eta$ and $f_t$. With the decrease in $\alpha$ there is a transition from a regime where the value of $\Phi$ is dominated by fluctuations, due to random movement of the foragers, to higher values of $\Phi$. The actual values of $\Phi$ are low because of the movements being restricted to the lattice. When $n = N$, the simultaneous discoveries are less and after the consumption of one cluster the foragers mostly execute RWs until a new cluster is detected. This causes the decrease in the value $\Phi$.

We analyse the collective effects on the individual foragers from the distribution of the length of the TWs, $P(l)$. Long TWs become more probable as $\alpha$ is reduced. We plot $P(l)$ against $l$, for different values of $m$ in Fig. 3(a), in the limit, $\alpha \to 0$. The plot reveals that for $m \geq m_c$, the walks become scale-free. For $n = N$, we find $P(l) \sim l^{-\mu}$ with $\mu = 2.80$ (using regression analysis). This also shows that for the emergence of scale-free walks, it is not necessary for foragers to have information about all the other foragers in the lattice. A TW initiated towards a targeted site, may get diverted towards a new site, when the targets at the original site are consumed, or when targets are discovered in nearer locations. A sequence of such diversions gives rise to very long walks.

We characterize the temporal heterogeneity in the behaviour of the foragers through the inter-event time distributions, $P(\tau)$, where, $\tau$ is the time between successive encounters with targets by the group, as a whole. As with $P(l)$, we evaluate $P(\tau)$ in the limit, $\alpha \to 0$. We observe from Fig. 3(b) that the states of the foragers become increasingly correlated as the size of the neighbourhood increases. The distribution $P(\tau)$ becomes fat tailed with increase in $m$. For $n = N$, we have, $P(\tau) \sim \tau^{-\delta}$, with $\delta = 1.67$.

**Figure 3.** (a) The plots of probability density function, $P(l)$, of the length of targeted walks, for $L = 512$, $N = 512$, $\gamma = 2.5$ and $\alpha = 0$. The different curves correspond to different values of $m$ (or $n$) as indicated in the legend. The dashed line is a guide to the eye and indicates the power-law nature in the region for the curve with $n = N$. Regression fit with $P(l) \sim l^{-\mu}$ gives the value of $\mu = 2.80$. (b) The plots of probability density function, $P(\tau)$, of waiting times between forager-target encounters, for $L = 512$, $N = 512$, $\gamma = 2.5$ and $\alpha = 0$. The different curves correspond to the same legend a in (a). The dashed line is a guide to the eye and indicates the power-law nature in the region for the curve with $n = N$. Regression fits with $P(\tau) \sim \tau^{-\delta}$ gives the value of $\delta = 1.67$. 
4. Discussion
Our model shows that when the target distribution is heterogeneous, collective effects among foragers can help enhance the efficiency of searching. The maximum efficiency is found to be in the case when each forager is equipped with the information about all the other foragers, but adopts a probabilistic strategy to follow only nearby foragers. However, in practice the radius of interaction would be finite and, at any instant of time, a forager would have information about only a limited number of other foragers. Our present investigation enumerates the efficient strategies when the neighbourhood is restricted to a finite radius. If the radius is small, then following other successful agents is always beneficial for a searcher. However, we find an optimal bound for this radius, dependent on the density of agents. Exchange of information above this length scale causes unnecessary aggregation at clusters of targets; and reduction in efficiency. In our model scale-free walks emerge as a result of the collective behaviour of the foragers. The presence of correlations in the behaviour of the foragers is also reflected in the scale-free inter-event time distribution. Overall, our model demonstrates the complexity that emerges when collective effects are incorporated into the behaviour of a set of agents which are involved in searching for targets. We believe that our model is representative of the foraging behaviour seen in animal groups and human populations [28, 29, 30, 31]. The model can also be of help from the viewpoint of design of artificial swarms [32, 33].

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References
[1] Girald%eau L A and Beauchamp, G 1999 Food exploitation: searching for the optimal joining policy Trends Ecol. Evol. 14 102
[2] Vickery W L, Girald%eau L A, Templeton J J, Kramer D L and Chapman C A 1991 Producers, scroungers, and group foraging Am. Nat. 137 847
[3] Champagne L, Carl RG and Hill R 2003 Search theory, agent-based simulation, and u-boats in the Bay of Biscay Proceedings of The 2003 Winter Simulation Conference I 991
[4] Coppey M, Bénichou O, Voituriez R and Moreau M 2004 Kinetics of target site localization of a protein on DNA: a stochastic approach Biophysical Journal 87 1640
[5] Bénichou O, Loverdo C, Moreau M and Voituriez R 2011 Intermittent search strategies Rev. Mod. Phys. 83 81
[6] Viswanathan G M, da Luz, M G E, Raposo E P and Stanley H E 2011 The physics of foraging (Cambridge, UK: Cambridge University Press)
[7] Turchin P 1998 Quantitative analysis of movement: measuring and modelling population redistribution in animals and plants (Sunderland, USA: Sinauer Associates)
[8] Bartumeus F and Catalan J 2009 Optimal search behaviour and classic foraging theory J. Phys. A: Math. Theor. 42 434002
[9] Viswanathan G M, Afanasyev V, Buldyrev S V, Murphy E J, Prince P A and Stanley H E 1996 Lévy flight search patterns of wandering albatrosses Nature 381 413
[10] Sims D W et al. 2008 Scaling laws of marine predator search behaviour Nature 451 1098
[11] Viswanathan G M, Buldyrev S V, Havlin S, da Luz M G E, Raposo E P and Stanley H E 1999 Optimizing the success of random searches Nature 401 911
[12] Bartumeus F, Catalan J, Fulco U L, Lyra M L and Viswanathan G M 2002 Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies Phys. Rev. Lett. 88 097901
[13] Bartumeus F, da Luz M G E, Viswanathan G M and Catalan J 2005 Animal search strategies: a quantitative random-walk analysis Ecology 86 3078
[14] James A, Plank M J and Edwards A M 2011 Assessing Lévy walks as models of animal foraging J. R. Soc. Interface 8 1233 and references therein.
[15] Raposo E P, Buldyrev S V, Da Luz M G E, Santos M C, Stanley H E and Viswanathan G M 2003 Dynamical robustness of Lévy search strategies Phys. Rev. Lett. 91 240601
[16] James A, Plank M J and Brown R 2008 Optimizing the encounter rate in biological interactions: ballistic versus Lévy versus Brownian strategies Phys. Rev. E 78 051126
[17] Pitcher T J, Magurran A E and Winfield I J 1982 Fish in larger shoals find food faster Behav. Ecol. Sociobiol. 10 149
[18] Haney J C, Fristrup K M and Lee D S 1992 Geometry of visual recruitment by seabirds to ephemeral foraging flocks Ornis Scandinavica 23 49
[19] Beauchamp G 2008 A spatial model of producing and scrounging Anim. Behav. 76 1935
[20] Tania N, Vanderlei B, Heath J P and Edelstein-Keshet L 2012 Role of social interactions in dynamic patterns of resource patches and forager aggregation Proc. Natl. Acad. Sci. 109 11228
[21] Torney C J, Berdahl A and Couzin I D 2011 Signalling and the evolution of cooperative foraging in dynamic environments PLoS Comput Biol 7 e1002194
[22] Boyer D, Miramontes O, Ramos-Fernández G, Mateos J L and Cocho G 2004 Modeling the searching behavior of social monkeys Physica A 342 329
[23] Martínez-García R, Calabrese J M, Mueller T, Olson K A and López C 2013 Optimizing the search for resources by sharing information: Mongolian gazelles as a case study Phys. Rev. Lett. 110 248106
[24] Bhattacharya K and Vicsek T 2014 Collective foraging in heterogeneous landscapes J. R. Soc. Interface 11 20140674
[25] Boyer D, Ramos-Fernández G, Miramontes O, Mateos J L, Cocho G, Larralde H, Ramos H and Rojas F 2006 Scale-free foraging by primates emerges from their interaction with a complex environment Proc. R. Soc. Lond. B 273 1743
[26] Fauchald P 1999 Foraging in a hierarchical patch system Am. Nat. 153 603
[27] Vicsek T, Czirók A, Ben-Jacob E, Cohen I and Shochet O 1995 Novel type of phase transition in a system of self-driven particles Phys. Rev. Lett. 75 1226
[28] Rand A L 1954 Social Feeding Behavior of Birds Fieldiana Zool. 36 5
[29] Clay Z and Zuberbühler K 2009 Food-associated calling sequences in bonobos Anim. Behav. 77 1387
[30] Galef Jr B G and Girardeau L A 2001 Social influences on foraging in vertebrates: causal mechanisms and adaptive functions Anim. Behav. 61 3
[31] Mangel M and Clark C W 1983 Uncertainty, search, and information in fisheries J. Cons. int Explor. Mer 41 93
[32] Dai H 2010 Design of adaptive collective foraging in swarm robotic systems (Kalamazoo, MI, USA: Western Michigan University)
[33] Winfield A F T 2009 Foraging robots Encyclopaedia of Complexity and System Science (New York: Springer) p 3682