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On the intermittent behaviour of foraging animals

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Abstract. – Many foragers adopt an intermittent searching behaviour in which active local search phases randomly alternate with relocation phases. The average duration of the searching phases has a power-law dependency upon the average duration of the relocation phases. Here it is shown that this observed power-law scaling can be understood within the context of an optimal scale-free (Lévy-flight) searching strategy.

Many foragers (*e.g.* plankitovorous fish, ground foraging birds and lizards) adopt an intermittent searching behaviour in which active local search phases randomly alternate with relocation phases [1,2]. The average duration of the searching phases, τ_1, and the average duration of the relocation phases, τ_2, obey the scaling relation $\tau_2 \propto \tau_1^p$ [3]. For foragers that spend more time searching than moving $p = 0.6 \pm 0.1$ whilst for foragers that spend more time moving than searching, $p = 0.7 \pm 0.1$. Recently Bénichou *et al.* [3] presented a kinetic model for the movement patterns of foragers that adopt intermittent searching strategies. In this model, active search phases (Brownian motion phases) randomly alternate with fast relocation phases (ballistic motion phases). They showed that the observed power-law scaling is predicted by their model when model parameters are chosen to minimize the mean searching time and so optimize searching efficiency. Here it is shown that the observed power-law scaling is also consistent with the adoption by the foragers of an optimal scale-free (Lévy-flight) searching strategy [4]. Lévy-flights associated with optimal scale-free searching strategies are known to capture essential characteristics of the movement patterns of many foragers including albatrosses, deer and bumblebees [4]. This new result illustrates how the scale-free and intermittent characteristics of animal movement patterns can be understood within a single, unified approach.

In the standard model of scale-free searching [4], a searcher moves in a straight line to the nearest target site if the site lies within a "direct vision" distance, r. If there is no target site within the distance r, then the searcher chooses a direction at random and a distance l drawn from a Lévy distribution, $P(l) = (\mu - 1)\,\theta\,(l - l_*)\,l_*^{\mu-1} l^{-\mu}$, where $1 < \mu \leq 3$ and where $\theta(x) = 1$ if $x > 0$ and 0 otherwise. The searcher then moves incrementally to the new location, constantly looking for a target within the radius r. If it does not detect a target site after traversing the distance l then it chooses a new direction and a new distance and continues
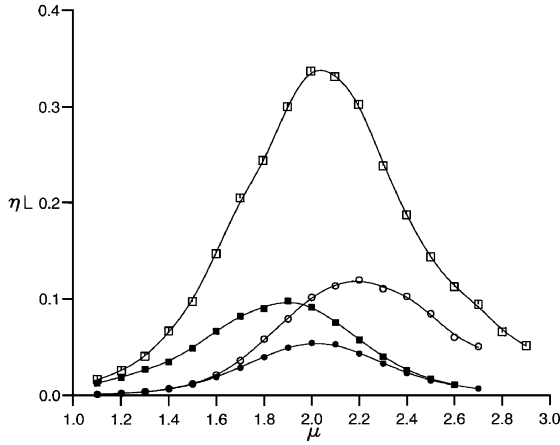

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Fig. 1 – Simulation data for the product of the mean target spacing L and the searching efficiency, η (*i.e.* the reciprocal of the mean distance traveled before location of a target site) of the scale-free model of intermittent searching. The target sites form a one-dimensional periodic arrangement with spacing $L = 10^4 l_*$, where l_* is the length of the shortest Lévy flight-segments. Simulation data is shown for destructive searching with $l_0/l_* = 50$ (●) and 1000 (■), and for non-destructive searching with $l_0/l_* = 50$ (○) and 1000 (□). The lines are added to guide the eye. In destructive searching, previously visited target sites are no longer target sites and searches effectively begin mid-way between adjacent target sites. In non-destructive searching, previously visited target sites remain target sites and searches effectively begin in the immediately vicinity of a previously visited target site. Optimal searching strategies are attained when $\mu \approx 2$. This exponent characterizes the movement patterns of albatrosses, deer and bumblebees [4].

searching, otherwise it proceeds to the target site. Time does not enter into the scale-free model explicitly but can be accounted for, trivially, by endowing the searchers with a speed.

Viswanathan *et al.* [4] defined the searching efficiency, $\eta = 1/L$, to be the reciprocal of the mean distance traveled before first encountering a target site. The optimal "non-destructive" searching strategy for the location of randomly and sparsely ($L/r \to \infty$) distributed targets is attained when $\mu = 2$. When the searching is non-destructive previously visited target sites remain target sites and new searches effectively begin in the immediate vicinity of a previously visited target site. The optimal "destructive" searching strategy arises as $\mu \to 1$ which corresponds to linear ballistic motion. In a destructive search previously visited target sites are no longer target sites and new searches effectively begin mid-way between adjacent, previously unvisited target sites.

Viswanathan *et al.* [4] did not attempt to describe in detail the complex biological mechanisms underlying target sensing. Here, the degradation of perception abilities with motion is incorporated into the model by allowing targets sites to be detected only during the execution of short flight-segments having lengths $l < l_0$. Flight-segments with lengths $l < l_0$ are thereby exclusively associated with the "searching phase" whilst flight-segments with length $l \geq l_0$ are exclusively associated with a "relocation phase" during which target sites cannot be detected. The spatial scale of the searching phase, l_0, is species-specific and dependent upon the perceptional abilities of the forager. The searching efficiency is, of course, optimal with respect to l_0 when $l_0/r \to \infty$ (*i.e.* when there is no degradation in perception abilities with motion) but such an optimal may not be attained in practice because of motion-induced perceptional degradation.
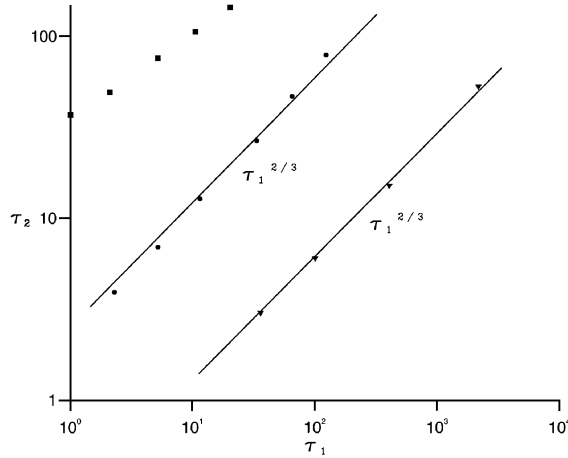
Fig. 2 – Simulation data for the average durations of searching and relocation phases associated with scale-free searching strategies having $\mu = 1.5$ (■), $\mu = 2$ (●) and $\mu = 2.5$ (▼). Searchers were initially located mid-way between two consecutive target sites forming a one-dimensional periodic arrangement with spacing $L = 10^4 l_*$ where l_* is the length of the shortest Lévy flight-segments. Simulation data is shown for $l_0/l_* = 100, 200, 500, 1000$ and 2000 ($\mu = 1.5$); $l_0/l_* = 10, 50, 100, 200, 500$ and 1000 ($\mu = 2$) and; $l_0/l_* = 100, 200, 500$ and 2000 ($\mu = 2.5$). The scaling $\tau_2 \propto \tau_1^{2/3}$ is indicated (solid lines). The distribution of segment lengths $P(l)$ was truncated at $l = 10^2 L$. Almost identical predictions were obtained with $l = 10L$. The scaling $\tau_2 \propto \tau_1^{2/3}$ does not depend upon the choice for the two speeds associated with the searching and relocation phases.

In this new model of scale-free searching, searching phases alternate randomly with relocation phases. The movement patterns of many foragers are characterized by such intermittency [1,2]. In these cases the searching phases tend to be associated with slow speeds whilst relocation phases tend to be associated with high speeds [2]. This observational characteristic can be incorporated into the model by assigning a relatively low speed to the short flight-segments ($l < l_0$) and by assigning a relatively high speed to the long flight-segments ($l \geq l_0$).

A searching (relocating) phase may consist of a single flight-segment with $l < l_0$ ($l \geq l_0$) or finitely many consecutive flight-segments with $l < l_0$ ($l \geq l_0$). Convergence of the mean length (duration) of the relocation phase can be guaranteed by introducing an upper bound, l_{max}^* on flight-segment length. In practice, energy consumption and territorial considerations will place an upper bound of the length of a flight-segment. The results of numerical simulations indicate that the exponent μ characterizing the optimal searching strategy and the scaling exponent p do not depend sensitively upon l_{max}^* when $l_{max}^* \geq 10L$, where L is the mean distance between target sites.

The simulation data presented in fig. 1 shows that the searching efficiency, η, of the new model of scale-free searching is optimal when $\mu \approx 2$; whenever $l_0/L < 1$ and irrespective of whether the searching is non-destructive so that target sites can be repeatedly revisited or destructive so that previously visited target sites are no longer target sites. Figure 2 shows that the average durations of the searching and relocation phases associated with scale-free searching strategies are well represented by $\tau_2 \propto \tau_1^{2/3}$ when $\mu \geq 2$. This scaling is attained when searchers spend more time searching than moving ($\tau_1 > \tau_2$) and when searchers spend more time moving than searching ($\tau_2 > \tau_1$). Departures from this scaling only become evident

when the cut-off length l_0 becomes comparable with or longer than the mean distance between adjacent target sites. When $\mu < 2$, $\tau_2 \propto \tau_1^p$ where $p < 2/3$.

In summary, it has been shown that the scaling relation $\tau_2 \propto \tau_1^{2/3}$ characterizing the durations of the searching and relocation phases of many foraging animals (*e.g.*, plankitovorous fish, ground foraging birds and lizards) is consistent with the adoption of an optimal scale-free searching strategy. This suggests that the scale-free and intermittent characteristics of forager movement patterns can be understood within the context of a single unified scale-free model. The scaling relation is also consistent with the adoption of an optimal two-state searching strategy [3]. It is hoped that this coincidence will motivate further experimental research to determine which model provides the better description of animal foraging behaviours. In this light it is worth noting that fruit-flies (*Drosophila*) are perhaps the most intensively studied intermittent searchers. For fruit-flies the distributions of durations of the searching and relocation phases obey an inverse square law over about one decade [5]. The inverse square law is compatible with the adoption of an optimal ($\mu = 2$) scale-free searching strategy.

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