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Deterministic walks with inverse-square power-law scaling are an emergent property of predators that use chemotaxis to locate randomly distributed prey

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The results of numerical simulations indicate that deterministic walks with inverse-square power-law scaling are a robust emergent property of predators that use chemotaxis to locate randomly and sparsely distributed stationary prey items. It is suggested that chemotactic destructive foraging accounts for the apparent Lévy flight movement patterns of *Oxyrrhis marina* microzooplankton in still water containing prey items. This challenges the view that these organisms are executing an innate optimal Lévy flight searching strategy. Crucial for the emergence of inverse-square power-law scaling is the tendency of chemotaxis to occasionally cause predators to miss the nearest prey item, an occurrence which would not arise if prey were located through the employment of a reliable cognitive map or if prey location were visually cued and perfect.

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I. INTRODUCTION

Over recent years, there has been an accumulation of evidence from a variety of experimental, theoretical, and field studies that many organisms have Lévy flight (LF) movement patterns when they are searching for resources [1–8]. Here and throughout, and in common with animal movement literature, the phrase "LF movement pattern" is used to refer to movement patterns either deterministic or stochastic that have power-law scaling characteristics. The analysis and interpretation of animal movement data is, however, not wholly straightforward and some of the analyses claiming Lévy flight patterns have recently been called into question [9]. The issue is hotly contested, and debate about the reliability of methods used to test for the presence of power-law scaling may continue for some time [9,10]. Central to a resolution of the issue is the identification of underlying processes that can give rise to LF movement patterns. The key to prediction and understanding does, after all, lie in the elucidation of mechanisms underlying the observed patterns [11]. Progress in this direction is being made. For example, Boyer *et al.* [12] showed that LF movement patterns can arise with destructive predators whose location rule is to minimize the quantity l_{ij}/k_i, where l_{ij} is the distance separating randomly located food items, i and j, whose sizes, k_i, are power-law distributed. In a destructive search, food items once visited are depleted. The mechanism identified by Boyer *et al.* [12] may account for the LF movement patterns of spider monkeys [13]. Santos *et al.* [14] consequently showed that LF movement patterns can arise with destructive predators whose location rule is always to travel to the nearest prey item when their movements are confined to a landscape consisting of a striplike region. More recently, it has been suggested that the LF movement patterns of jackals [3] and the fractal movement patterns of beetles [15] can be attributed to conspecific odor trail avoidance (a behavior designed to avoid locations previously traversed by individuals of the same species, a trait first identified in carabid beetles [16]) [17]. The LF patterns of airborne male moths [18] may also have an olfactory basis and stem from a naive response to turbulent fluctuations in the concentrations of attractive odor dispersing within the atmospheric boundary layer [19]. Additionally, it has been conjectured that LF movement patterns in *Drosophila* fruit flies have a neurological basis [5]. This convergence of behaviors along such different evolutionary pathways is not surprising given the energetic efficiencies that Lévy flight movement patterns confer.

Here we report on a novel olfactory mechanism for the occurrence of LF movement patterns. Through the use of numerical simulations, we show that deterministic walks with inverse-square power-law scaling are an emergent property of predators that use chemotaxis to locate randomly and sparsely distributed stationary prey items. In this scenario, the prey act as sources of chemoattractant and the attractant diffuses throughout the surrounding landscape. Upon arriving at a prey item, the predator destroys that source of chemoattractant. It is suggested that this mechanism accounts for the $\mu \approx 2$ LF movement patterns observed in *Oxyrrhis marina* microzooplankton in still water containing sparsely and randomly distributed prey [4]. *O. marina* microzooplankton use chemotaxis to locate their prey [20] and forage destructively. The model and analysis of the simulation is presented in the next section, and is followed by a discussion.

II. MODEL FORMULATION AND THE EMERGENCE OF LF MOVEMENT PATTERNS

Concentrations of chemoattractant, c, undergo Brownian diffusion and evolve in time, t, and two-dimensional space, x,y, according to the standard diffusion equation

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2} + D\frac{\partial^2 c}{\partial y^2} + q(x,y), \tag{1}$$

where D is the diffusivity of the chemoattractant and $q(x,y)$ are the release rates of chemoattractant from randomly distributed sources (prey items). A discrete form of Eq. (1) was

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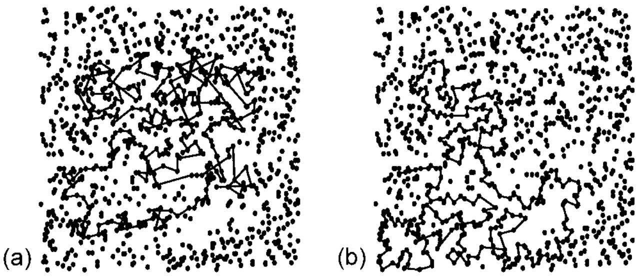

FIG. 1. (a) An example movement pattern of a predator using chemotaxis to locate randomly distributed prey items. (b) An example movement pattern of a predator whose location rule is always to move to the nearest prey item.

solved numerically. Forward differencing was used for the time derivatives, and central differencing was used for the spatial derivatives. At the boundaries of the computational domain (i.e., the "landscape" containing the prey), concentrations of chemoattractant vanish so that $c=0$. Model predictions do not depend sensitively on the boundary condition $c=0$ because all analyses were restricted to movements that did not approach the boundaries of the computational domain.

Unless stated otherwise, the numerical simulations were performed on landscapes of size $200\Delta x \times 200\Delta y$, initially containing 1000 randomly located prey items that first became active at the start of the search and which release chemoattractant at a constant rate, $q=\Delta t^{-1}$. Here Δt, Δx, $\Delta y=\Delta x$ are the sizes of the temporal-spatial steps used in the numerical integration of the discrete form of the diffusion equation (1). The diffusivity $D=0.1\Delta x^2 \Delta t^{-1}$. The distribution of prey items is the only source of randomness. Predators use a purely deterministic algorithm and simply move in the direction in which the gradient of chemoattractant is largest. A prey item is located when the predator enters the computational cell containing the prey item. The movement patterns considered here do not represent the continuous movements of a predator but instead are formed from straight-line "moves" that join together successive prey items located by the predator. These locations, in contrast with the locations of other much smaller changes in direction, are biologically significant.

An example of a movement pattern of a predator using chemotaxis to locate randomly distributed prey items is shown in Fig. 1(a). The predator starts from the center of the landscape and searches for a time $2\times 10^4 \Delta t$. Around 35% of the prey items are located within this time span. Chemotaxis tends to direct a predator to the nearest prey item [Fig. 1(a)]. Occasionally, however, attraction to a local cluster of prey can be greater than to the single nearest prey item, and in these instances the nearest prey is not visited by the predator but instead remains a target for a later stage in the search. The movement patterns of these predators are therefore fundamentally different from predators whose location rule is always to travel to the nearest prey item [Fig. 1(b)], and this crucial distinction leads to scaling behaviors that are different from those identified by Santos *et al.* [14]. It is evident from Fig. 1(a) that frequently occurring but relatively short moves between successive prey items are punctuated by more rarely occurring longer moves. The distribution of move lengths of chemotactic predators can, in fact, be accurately represented by an inverse-square power-law [Fig. 2(a)]. This distribution, P_l, was obtained by ensemble-averaging over 50 searches, the sizes of the data collection bins were logarithmically distributed, and the numbers of straight-line movements have been normalized by the bin sizes. The linear regression of log P_l on log l gives a best-fit exponent -2.1 ± 0.05 ($r^2=0.92$). The inset shows the same distribution on log-linear scales. The high tail is clearly nonexponential. The emergence of inverse-square power law scaling is highly significant because it is often taken to be indicative of the presence $\mu=2$ LF in animal movement patterns. Crucial for the emergence of an inverse-square power law by this mechanism is the tendency of chemotaxis to occasionally cause predators to miss the nearest prey item, an occurrence that would not arise if searching were visually

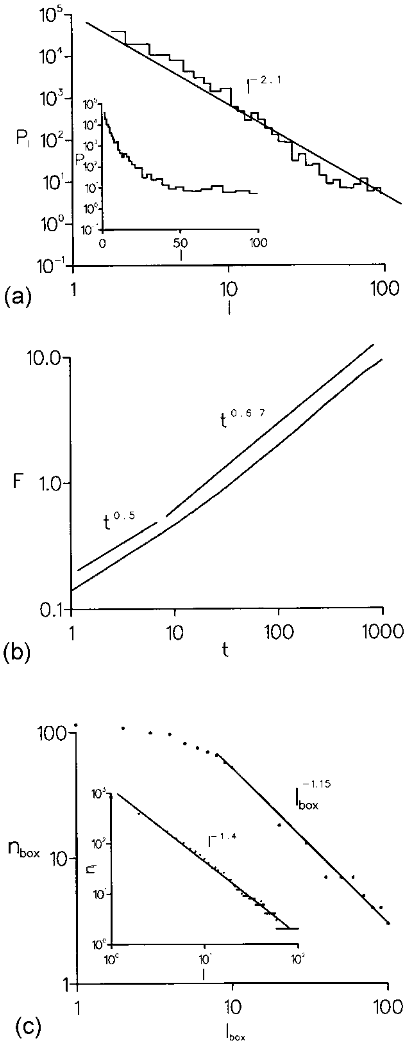

FIG. 2. (a) The distribution P_l of the move lengths l of chemotactic predators. (b) An example of the root-mean-square value of the running sum, F, for a chemotactic predator movement pattern. (c) Fractal scaling properties of a chemotactic predator movement pattern revealed by the box-counting method and by the dividers method (inset).

cued and perfect, or if reliable cognitive maps were utilized [12]. In the latter case, movement patterns are Gaussian [12].

Further evidence for the emergence of power-law scaling characteristics from chemotaxis comes from the results of a "random-walk" analysis, which can detect the presence of scale-free characteristics. In this analysis, the time series $u(t)$ of the numbers of prey items located (i.e., the number of turning points of biological significance in the movement pattern) within time intervals t to $t+\Delta t$ are treated as increments in a random walk where the net "displacement" is just the running sum $n(t)=\Sigma_{i=0}^{N=t/\Delta t}u(i)$. An important statistical property characterizing the walk is the root-mean-square fluctuation of the displacement $F(t)=\sqrt{\langle[\Delta n(t)-\langle\Delta n(t)\rangle]^2\rangle}$, where $\Delta n(t)\equiv n(t_0+t)-n(t_0)$ and where the angular brackets denote an ensemble over all possible times t_0. If the values of $u(t)$ are completely uncorrelated and behave like "white noise," then the root-mean-square displacement $F\propto t^{\alpha}$, where $\alpha=\frac{1}{2}$. Markov process also gives rise to $\alpha=\frac{1}{2}$ for sufficiently large t. Time series with long-range correlations having no characteristic scale are, however, characterized by $F\propto t^{\alpha}$ with $\alpha\neq\frac{1}{2}$ [21]. Figure 2(b) shows that chemotaxis is characterized by $\alpha=0.61\pm0.09$ (the error is found by estimating α for 50 different time series via least-squares regressions of log F on log t for times t between $10^1\Delta t$ and $10^3\Delta t$; a predator can locate approximately 100 prey items within this time span). This scaling implies that long term power-law correlations exist in the motions of a chemotactic predator. The scaling differs from that of finitely long $\mu=2$ LF movement patterns, which are characterized by $\alpha=0.80\pm0.05$ [1]. The distinction may arise because the speed of the predator is not constant so that distances traveled and times of flight (movements between consecutively located prey items) are not strictly interchangeable. Predators can, for instance, become temporally trapped close to a recently extinguished prey item and only escape when locally produced concentrations of chemoattractant have diffused away. This trapping effect may also account, at least in part, for the presence of Brownian-like motions at short times [Fig. 2(b)]. The positions of prey items located during a well-developed search do, however, have fractal dimension, $D=1.15\pm0.07$ [Fig. 2(c)], and this speed-independent quality is compatible with that of finitely long $\mu=2$ LF movement patterns [6,7]. Figure 2(c) shows the average number, n_{box}, of boxes required to enclose the prey items that were located by a chemotactic predator between times $5\times10^3\Delta t$ and $1\times10^4\Delta t$ as a function of the box size, l_{box} (measured in units of Δx). A power-law relationship of the form $n_{\text{box}}\propto l_{\text{box}}^{-D}$ would be indicative of a scale-free characteristic with fractal dimension D, and here, a linear least-squares fit shows that $D=1.15$ ($r^2=0.89$). The inset shows the presence of fractal scaling as revealed by the dividers method. In this method, the number of steps, n_l, taken by dividers of length l when moving along a movement path is calculated. A power-law relationship of the form $n_l\propto l^{-D}$ would be indicative of a scale-free characteristic with fractal dimension D, and here, a linear least-squares fit shows that $D=1.4$ ($r^2=0.98$).

The results of numerical simulations indicate that the emergence of deterministic walks with inverse-square power-law scaling from chemotactic destructive foraging is not dependent on the geometry and the dimensionality of the landscape within which the predator moves. This contrasts with predators whose movement rule is always to move to the near prey item. In this case, inverse-square power-law scaling is only attained in narrow strip geometries [14]. The emergence of inverse-square power-law scaling may also be insensitive to both the distribution of source strengths [Fig. 3(a)] and the age of the sources [Fig. 3(b)], and in this sense may be a robust characteristic of chemotactic destructive foraging. Power-law scaling does, however, become less apparent in the later stages of the search when the density of the remaining prey items is low [Fig. 3(c)]. Nevertheless, inverse-square power-law scaling is present and becomes evident when ensemble-averaging over many searches [Fig. 3(d)]. The results of numerical simulations also indicate that the emergence of inverse-square power-law scaling does not depend sensitively on the speed of the predator. This may be because the trapping that arises temporally in the vicinity of a recently consumed prey item is the rate-limiting process. Even when traveling at very high speeds, concentrations of chemoattractant may become relevant far from prey items before the predator can move away from the first consumed prey item. Without this trapping, it is likely that high-speed predators would always move to the nearest prey item.

Power law scaling does not arise when consumed prey items are replaced by new prey items that appear at random locations so that the total number of prey items within the landscape remains constant. The emergence of power-law scaling is therefore dependent on a continual depletion of prey numbers. This is realistic when foraging is destructive and must arise in the experimental studies of microzooplankton [4] that motivated the current theoretical study. It is also crucial that prey items are randomly distributed because a chemotactic predator moves sequentially between regularly spaced prey and because power-law scaling is not evident when prey items are patchily distributed (Fig. 4). In the presence of patchily distributed prey, the movement patterns of chemotactic predators are akin to optimal *adaptive* LF searching patterns [22,23] that are comprised of straight-line movements between patches (corresponding to LF movement patterns with $\mu\rightarrow1$) and Brownian movement patterns within patches. It is evident that in chemotactic foraging, the imposition of a behavioral rule like the "giving up distance" is not required to invoke patch departure prior to complete depletion of local prey items (Fig. 4). This incomplete depletion can lead to the predator revisiting a patch.

III. DISCUSSION

The results of numerical simulations indicate that deterministic walks with inverse-square power-law scaling are an emergent property of destructive foragers employing chemotactic gradient following to locate randomly and sparsely distributed prey items. Inverse-power square-law of movement lengths was evident over about two decades [Fig. 2(a)] and was supported by power-law scaling of a time-series analysis of the turning points extending over about two decades [Fig. 2(b)], and by fractal scaling over about one decade [Fig. 2(c)]. The walks are deterministic rather than stochastic because they are determined *a priori* by the particular arrange-

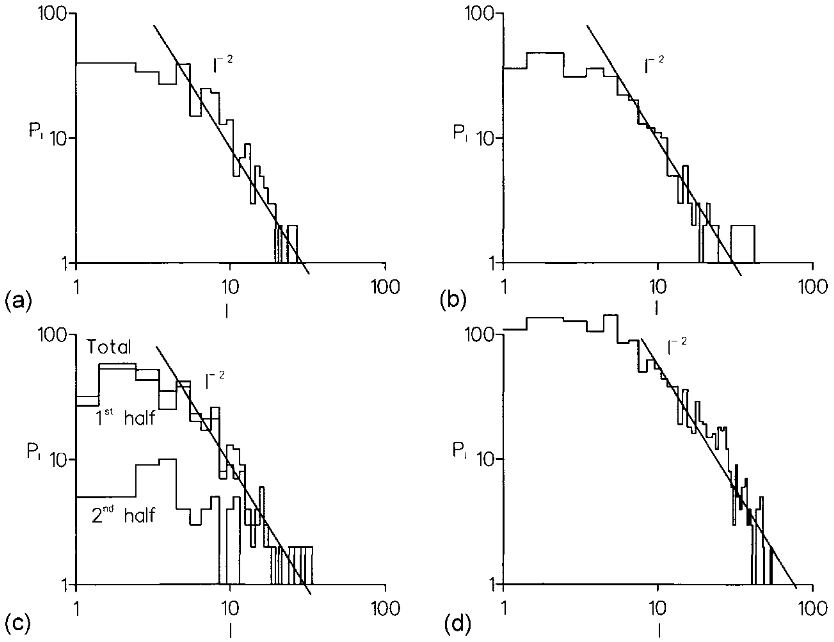

FIG. 3. (a) An example of the distribution of the move lengths of a chemotactic predator moving within a landscape containing prey items having chemoattractant release rates, q, randomly distributed between 0 and Δt^{-1}. (b) An example of the distribution of the move lengths of a predator moving within a landscape containing prey items that first began emitting chemoattractant at times randomly and uniformly distributed between the start of the search and $1\times10^4\Delta t$ before its commencement. (c) The distribution of move lengths for the first and second halves of a search, and for the total search. (d) An example of the ensemble distribution of move lengths of 20 chemotactic predators moving within 20 different landscapes during the second halves of their searches.

ment of prey items within the landscape. Their power-law scaling and fractal properties are, nevertheless, indistinguishable from that of random $\mu=2$ LF movement patterns.

Chemotactic destructive foraging may underlie the apparent presence of $\mu\approx2$ LF movement patterns of microzooplankton *M. Oxyrrhis* in still water containing prey that have been observed in a Palmer cell (18 mm diameter and 0.4 mm deep), a pseudo-two-dimensional landscape akin to that investigated in the numerical simulations [4]. This possibility reinforces the view that the movement patterns microzooplankton do, indeed, exhibit inverse-square power-law scaling but it also challenges the notion that this scaling stems from the execution of an innate, evolved LF searching strategy. The issue can be resolved by careful reexamination of the high tail of the distribution of the move lengths. In chemotactic gradient following the high-tail is an inverse-square power-law while in a LF search it will be exponential, due to LF movement patterns being randomly truncated following detection of prey items. Alternatively the issue would be resolved if starved microzooplankton were found to have LF movement patterns in the absence of prey items (sources of chemoattractant) because that would rule out chemotactic destructive foraging as being the underlying mechanism.

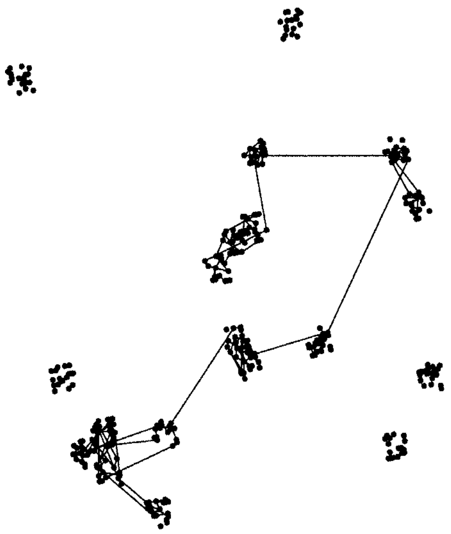

FIG. 4. An example movement pattern of a predator using chemotaxis to locate patchily distributed prey items. The landscape initially contains 20 randomly located patches each comprised of 20 randomly distributed prey items.

The foregoing analysis may provide new insights into the foraging behaviors of microzooplankton. For instance, when confronted with a variety of chemical stimuli (i.e., from a mixed-prey assemblage), *M. Oxyrrhis* seem unable to discern the difference between cues that originate from high and poor quality (or even toxic) prey items [20]. Our analysis indicates that the poor quality prey items could serve as markers for locations at which microzooplankton must change direction if they are to execute pseudorandom $\mu=2$ LF searching patterns for the location of high quality food items. This strategy would be effective even when attempting to locate prey items that themselves are not sources of chemoattractant. Such movement patterns constitute an optimal LF searching strategy for the location of sparsely and randomly distributed prey items [24]. The foregoing analysis may also provide new insights into the movement patterns of subterranean invertebrates. This area of research has received little attention but is of considerable importance when attempting to understand and to predict the important role that invertebrates play in soil ecosystems by mediating nutrient turnover, inflicting damage on crops, benefiting plants by consuming pathogenic microorganisms, and by transporting otherwise relatively immobile organisms through the soil. It has long been recognized that chemotactic gradient following is the primary means by which soil dwelling organisms locate hosts and prey. The subterranean hexapod collembola, *Protaphorura armata*, for instance, utilizes chemical cues to discriminate among food sources [25,26]. These observations together with our theoretical analysis suggest that some subterranean invertebrates have movement patterns akin to $\mu=2$ LF. This possibility has not been explored and warrants investigation.

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