THE GEOMETRY OF FORAGING PATTERNS: COMPONENTS OF THOROUGHNESS IN RANDOM SEARCHING

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Abstract. A Monte Carlo simulation of the movements of a randomly-searching predator was used to develop a novel geometrical measure, the "thoroughness" of the search, and to investigate the effects of meander, turn asymmetry, and path length. Thoroughness varied directly with the meander and the square of the asymmetry measure and remained relatively invariant with path length. The regularity of its relationship to the generating parameters of the search and the ease with which it may be estimated from field data recommend thoroughness for use in characterizing empirical search patterns and in testing for the occurrence of systematic searching.

The foraging movements of many animals can be approximated by a restricted or persistent random walk, in which the vector choice at each successive step is stochastically determined, subject to constraints on the probability of a change from the previous direction of movement (Barber & Ninham 1970; Murdie & Hassell 1973; Patlak 1953; Pyke 1978b). Any locomotory pattern that departs significantly from a random walk, particularly if it leads to the avoidance of areas that have been depleted of food, can be referred to as "systematic" search. It has occasionally been asserted that a random-walk strategy is "inefficient" in that it requires an animal to expend time and energy in the fruitless examination of areas that have previously been thoroughly searched, thereby decreasing the net area covered per unit of searching effort (Krebs 1973; Paloheimo 1971a,b).

Given the common assumption that the energetic efficiency of foraging tends to be maximized in the course of evolution (Pyke *et al.* 1977), this argument suggests that systematic search should be adaptive and that systematic components should be observable in the movement patterns of most actively-foraging species. However, this argument implicitly assumes that food resources are usually depleted on the first pass through an area, and that depleted resources do not regenerate rapidly enough to make a second pass profitable. Animals that take food that is concealed, cryptic, or otherwise difficult to detect, those that are inefficient in their attempts to capture prey, and those that feed on mobile and rapidly recovering resources, such as flying insects or plankton, are less likely to be critically affected by the amount of overlap in their search paths.

Even within the limits of the assumptions, avoidance of overlap cannot be the sole consideration in determining foraging efficiency. If this were the case, the optimal searching pattern for all animals would be a straight line. But strictly linear movement, insofar as it may be indirectly diagnosed from the occurrence of correcting behavior (Jander 1975), appears characteristic mainly of animals that search for coarse-grained resources, in which encounter with a single food patch alters or eliminates the need for further searching. Animals that must

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successively locate numerous items of a fine-grained resource commonly produce nonlinear, often highly convoluted search paths (Curio 1976; Krebs 1973). Where food resources are aggregated, such behavior probably serves to minimize the distance traveled between successive items and to prevent the animal from leaving regions of resource concentration (Jander 1975). The range or degree of excursion of the search as a function of the distance moved and its interaction with the pattern of distribution of the resource are therefore of primary importance in the assessment of foraging efficiency (Pyke 1978b).

Systematic searching also entails some costs, at least in terms of information processing. To successfully avoid overlapping search paths, an animal must be able to recognize areas it has previously covered, either by marking them in some fashion (Pyke 1978b; Baup & Seilacher 1969) or by remembering associated stimuli (Gill & Wolf 1977; Kamil 1978; 0lton & Samuelson 1976; Zach & Falls 1976). The only alternative to a recognition mechanism is a "motor program," a structured sequence of foraging movements, such as an expanding spiral (Kleerekoper *et al.* 1972, Raup & Seilacher 1969) or alternating turn directions (Jander 1975; Smith 1974), that prevents an animal from re-crossing its own trail. In each of these cases, the amount of information that must be processed and retrieved in the course of searching appears to be larger than that required by a restricted random walk. It is not obvious that the advantage of decreased overlap will invariably offset the costs of this increased complexity. This is especially true, given that random foraging has been shown to be capable of great flexibility in dealing with variation in the distribution and abundance of food. A random-walk process does not exclude the possibility of altering the generating parameters, such as the width of the search path, the step length, or the distribution of turn probabilities, in the course of searching either as a function of past experience or in response to immediate stimulation. By means of such modifications, foraging efficiency can be optimized, within limits, fitting the generated pattern to the distribution of the resource (Bond 1980; Curio 1976).

A quantitative estimate of the advantage of systematic over random searching in any given circumstance appears to require a measure that is affected by both overlap and path dispersal, that is simply and regularly related to the generating parameters of a random search, and that can readily be estimated from empirical data. If we define the net area searched as $N = Lw - O$, where L is the path length, w the path width, and O the area of overlap, one such measure is N/A, where A is the area of the minimum circumscriptive circle, the smallest circle that will just enclose all points on the search path. This ratio, which I have called "thoroughness" (θ), is maximized when the search path is space-filling, leaving few unexamined lacunae, and when overlaps are systematically avoided; it is minimized when the search path is linear. Given a functional relationship between thoroughness and the generating parameters of a random search, it should be feasible to compare experimental observations to a random-walk expectation to detect and quantify systematic elements in foraging behavior.

Simulation Methods

To determine the relationships between θ, A, and O and the generating parameters of a random search, we conducted a Monte Carlo simulation. Although some workers have used the analytical theory of random walks to explore searching behavior (Broadbent & Kendall 1953; Hassell & May 1974; Koopman 1956), realistic constraints on the vector choice at each step, particularly those involving persistence of direction across several successive steps, yield complex solutions that cannot readily be applied to empirical data (Paloheimo 1971a,b; Patlak 1953). To obtain a more tractable approximation to real-world phenomena, several authors have resorted to computer simulations of random search, either to provide a means for data analysis (Cody 1971; Jones 1976; Murdie & Hassell 1973; Pyke 1978a; Saila & Shappy 1963), or to examine changes in the properties of a search resulting from the use of

different sets of generating parameters (Beeler 1973; Pyke 1978b; Raup & Seilacher 1969; Rohlf & Davenport 1969; Siniff & Jessen 1969). There is a considerable body of literature, beginning with Koopman (1957) and reviewed and extended in Stone (1975), concerned with the question of searching efficiency and optimization, but only Pyke (1978b) and Cody (1971) have examined directly the effects of changes in the generating parameters of the search.

For the purposes of this study, random foraging behavior was simulated by movements among the cells of an unbounded hexagonal matrix, a two-dimensional array in which transfer to any of six equidistant positions is possible from any given point. The probability of a given deviation from the movement vector in the previous step was normally distributed about a pre-selected mean value, with a constant standard deviation of 16.22°. The mean deviation per step, termed the "meander," *m*, was given 11 values from 0° to nearly 90° in roughly equal increments. The asymmetry, *α*, defined as

$$\alpha \equiv \frac{|p-0.5|}{0.5} = |2p-1| = |p-q|,$$

where *p* and *q* represent the probability of a left or a right turn, respectively, was varied independently, taking the values 0, 1/3, 2/3 or 1. For each combination of asymmetry and meander, 300 paths of length *L* = 200 steps were generated. At intervals of 25 steps in each iteration, three output variables were calculated: the area of overlap, *O*, estimated by the number of returns to a previously-occupied cell; the diameter, *D*, of the circumscriptive circle, estimated by the perpendicular distance between opposite sides of the minimum circumscriptive hexagon; and the beeline distance, *B*, the minimum travel distance between the beginning and end points of the path. Given that the area, *A*, of the circumscriptive hexagon is related to its diameter by

$$A = \frac{3n_D^2 + 1}{4}, \qquad 1)$$

where n_D is the smallest odd integer $\geq D$, an estimate of thoroughness, θ, was derived for each combination of generating parameters. A sample search path, illustrating the calculation of the output variables, is provided in Fig. 1.

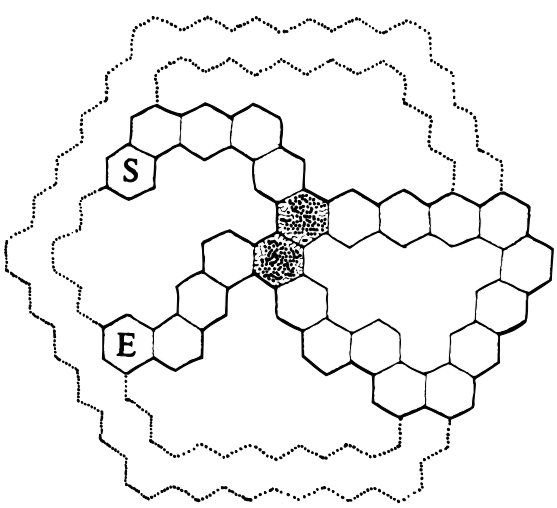

Figure 1. Sample search path from simulation. **S** = start; **E** = end. Input parameters: (α = 0; *m* = 34; *L* = 25. The minimum circumscriptive hexagon, outlined with dotted lines, has a diameter of 11 units and an area of 91. There were two overlapping cells (shown stippled). The thoroughness of this path is, thus, (*L* - *0*)/*A* = (25 -2)/91 = 0.253. The beeline distance is 4.

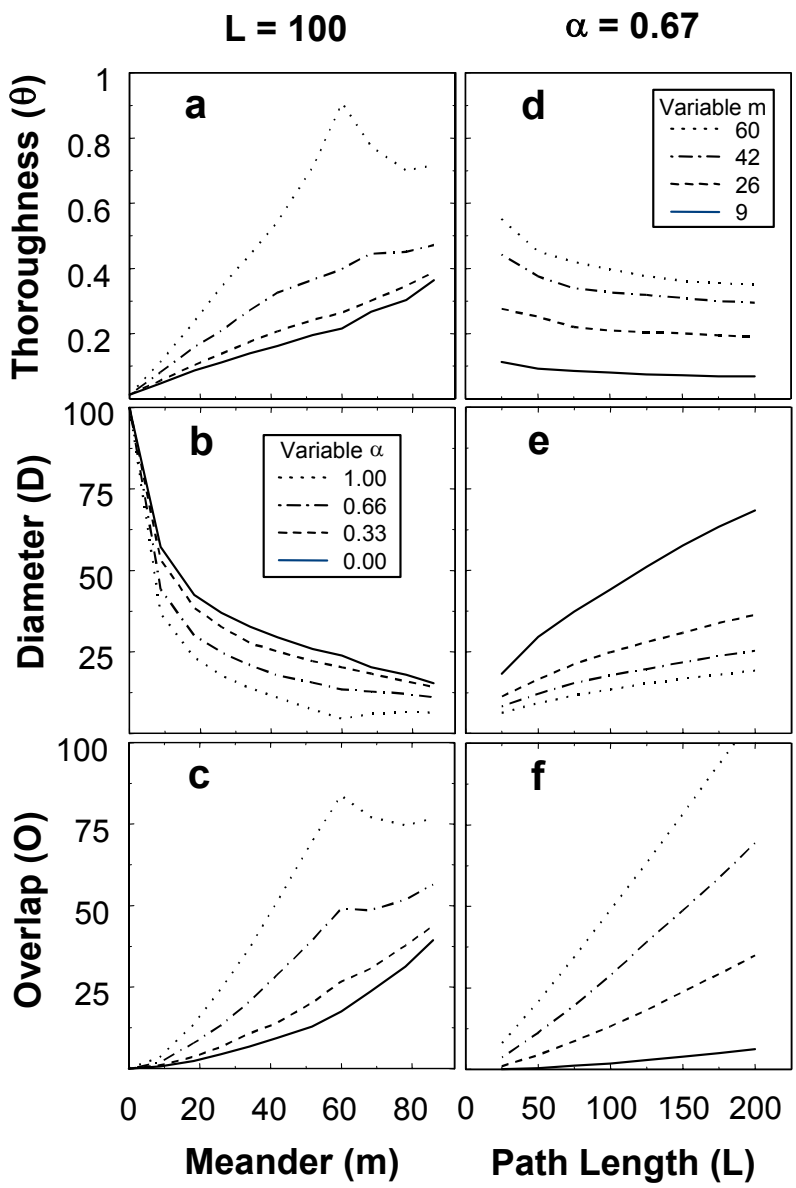

Figure 2. Functional relationships among simulation variables. **a-c**: Thoroughness, diameter, and overlap as a function of meander, in degrees per step, for four different levels of asymmetry. Path length was held constant at 100 steps. **d-f**: Thoroughness, diameter, and overlap as a function of path length at four different levels of meander. Asymmetry was held constant at 0.67.

Simulation Results

Means of thoroughness, diameter, and overlap for representative input values are graphed in Figs. 2a-f. It is apparent from Fig. 2a that θ increases monotonically with *m*, at least for $m \leq 60°$ / step. The decline in overlap and thoroughness above *m* = 60°, particularly at high α, is probably an artifact of the discrete model: *A* has a minimum value of 7 in an hexagonal matrix, where the path conforms to the smallest possible ring of cells. For *m* = 60°,

and $\alpha \geq 0.67$, this minimum ring is attained fairly often, yielding peak values for *O* and θ. Increasing *m* beyond this point cannot help but increase *A*, since a larger proportion of 120° turns will tend to spread the path and draw it away from the minimum ring. With increasing *A* at constant *L*, there is therefore a concomitant reduction in *O* and θ. There is no reason to suppose that the change in trend above 60° holds any meaning for the continuous case, and analysis of the output will be performed only within the region of monotonicity.

When *m* = 0, a strictly linear search path, θ attains its minimum value, *K*, which is a function of the path length. Given the relationship between area and diameter in Eq. 1,

$$K(L) = \frac{4L}{3n_L^2 + 1},$$

Since $n_L / L \to 1$ as *L* increases, *K* will approach zero with increasing path length:

$$K(L) \cong \frac{4}{3L + \frac{1}{L}} \approx \frac{4}{3L}. \qquad 2)$$

The form of the empirical functions in Fig. 2a strongly suggests that θ may approximate a simple linear relationship with *m*. In fact, for $L \geq 100$, a two-parameter least-squares fit to the equation

$$\theta = am\left(1 + b\alpha^2\right) \qquad 3)$$

accounted for 98.8% of the variance in θ, with coefficients of $a = 0.0023$ and $b = 3.66$. The quadratic component of *m* and the linear component of α were statistically significant but had only a trivial effect on the fit of the model. For $L < 100$, a path length term must also be included (Fig. 2d):

$$\theta = am\left(1 + b\alpha^2\right) + K(L) \qquad 4)$$

An alternative expression for θ, one that is not tied to model regression coefficients, can be obtained by viewing the *L* steps of the search path as being placed independently into the *A* cells of the minimum hexagon. In this case, the number of steps per cell can be considered a Poisson variate, with mean L / A. The probability of no steps, *s*, in a given cell would, therefore, be

$$P(s = 0) = \mathbf{e}^{-L/A},$$

and the probability of one or more steps would be

$$P(s \geq 1) = 1 - \mathbf{e}^{-L/A}.$$

The expected number of cells with one or more entries is then an expression for the net area searched,

$$N = A\left(1 - \mathbf{e}^{-L/A}\right),$$

which provides an equation for overlap as

$$O = L - A\left(1 - \mathbf{e}^{-L/A}\right).$$

Rearranging terms,

$$\theta \equiv \frac{L - O}{A} = 1 - \mathbf{e}^{-L/A}. \qquad 5)$$

An identical expression was derived by Koopman (1956) to describe the probability of encountering a target somewhere in an area *A* with a random search of length *L*. Using this approximation, the thoroughness of a random search can be estimated directly for the continuous case from a knowledge of the path length, the path width, and the diameter of the minimum circumscriptive circle:

$$\ln(1 - \theta) \approx -\frac{4Lw}{\pi D^2}. \qquad 6)$$

A measure of thoroughness can, thus, be derived even from fairly rough field observations and can be used as a null hypothesis to test for the occurrence of systematic components.

Additionally, the Poisson approximation and the regression equation for thoroughness (Eqns. 4 and 5) together yield expressions of *D* and *O* as functions of the path parameters that can be tested against the results of our simulation. If Eqs. 4 and 5 hold, then $F(m,\alpha,L) = \mathbf{e}^{-L/A}$ should also be roughly linear in *m*. The correlation between *F* and $1-\theta$ is 0.99, implying that the Poisson approximation should suffice to account for the model results. We can therefore fit the equation

$$F = K'(L) - a'm\left(1 - b'\alpha^2\right), \qquad 6)$$

where

$$K'(L) = \exp\left[\frac{4L}{3n_L^2 + 1}\right].$$

For $L \geq 100$, a least-squares fit to this equation accounted for 98.4% of the variance in *F*, with coefficients $a' = 0.00242$ and $b' = 5.18$.

Given that $-L/A = \ln(F)$, we can derive an expression for *D*:

$$A = -\frac{L}{\ln(F)} \approx \frac{3D^2 + 1}{4},$$

so

$$D \approx \left[-\frac{1}{3}\left(\frac{4L}{\ln(F)} + 1\right)\right]^{1/2}. \qquad 7)$$

The diameter is, thus, a square-root function of *L*, as is evident from Fig. 2e and consistent with analytical studies of random walks (Barber & Ninham 1970). Because *F* is a linear function of *m*, *D* varies as the square root of the inverse log of *m*: as *m* increases, ln(*F*) decreases at a rate that is inversely proportional to *m*. *D* is, therefore, a decreasing function of *m* with a gradually increasing slope (Fig. 2b).

An expression for overlap can be derived in a similar fashion. Since $O = L - A\theta$, $\theta = 1 - F$, and $A = -L \ / \ \ln(F)$,

$$O = L\left(1 + \frac{1-F}{\ln(F)}\right). \qquad 8)$$

Overlap is an approximately linear function of path length (Fig. 2f), but its relationship to *m* is more complicated. As *m* increases linearly, 1 - *F* increases linearly, and the absolute value of ln(*F*) increases at a decreasing rate. Because $0 < F < 1$ (by the assumption of the Poisson approximation), ln(*F*) is never positive, however, so *O* must be an increasing function of *m* with a gradually increasing slope (Fig. 2c). The consistency between the expressions derived for *O* and *D* and the results of the simulation model provide additional support for the legitimacy of our modeling approach.

Discussion

Optimal Path Parameters in a Bounded Search

Unless there are systematic elements in the search path, greater thoroughness can be obtained only at the cost of increasing the overlap and decreasing the dispersion. The efficiency of a particular random search strategy will therefore depend strongly on the pattern of distribution of the resource. For an evenly-distributed or coarse-grained resource, the dispersion component of thoroughness may be much less important than the overlap component, and the most efficient foraging pattern may approach a straight line. Resources occurring in widely-dispersed patches that lack natural borders or demarcations may demand an altogether different strategy, one involving an alternation of widespread, superficial sampling to locate a patch, followed by concentrated, intensive search within a localized region (e.g. Bond 1980). In the latter phase, the amount of overlap a search generates may be insignificant when compared to the need to confine the search to an area in which resources are relatively abundant. Foraging efficiency in these cases will be influenced jointly by the thoroughness of the intensive search phase and the duration or persistence of the search. Pyke (l978b) attempted to find path parameters that would maximize the thoroughness of a random search within a particular bounded region, while minimizing the amount of overlap. The expressions for thoroughness derived in this paper appear to provide a general solution to Pyke's optimality problem.

For any area *G* to be searched in *L* steps, the optimal meander, $\hat{m}$, is that which will generate, on the average, a minimum circumscriptive area of *G* in the given path length. That this is, in fact, an optimal solution can easily be demonstrated. Consider a higher meander value, m'. With a path of length *L*, it will cover a minimum circumscriptive area $A' < G$ and generate an area $O' > O$ of overlap. The thoroughness, as measured over the entire area *G*, would then be

$$\theta' = \frac{L - O'}{G} < \frac{L - O}{G}.$$

Similarly, a lower meander value, m'', will cover a minimum area $A'' > G$. The thoroughness measured over A'', θ'', will then be $< \theta$, by Eqn 4, and this reduction will apply as well to the included region, *G.*

The criterion of optimality, thus, is

$$F(\hat{m},\alpha,L) = \mathbf{e}^{-L/G}.$$

Using Eqn. 6 and solving for $\hat{m}$, we have

$$K'(L) - a'\hat{m}\left(1 + b'\alpha^2\right) = \mathbf{e}^{-L/G}, \text{ or}$$

$$\hat{m} = C\left|K'(L) - \mathbf{e}^{-L/G}\right|.$$

The optimal meander is thus an exponential function of 1/*G*, and corresponding values of the other generating parameters can be derived in a similar fashion. It is possible to argue that the intensive searching that commonly follows patch discovery should display a joint optimization of persistence and meander that will maximize the net rate of energy intake for the particular conditions of patch area, richness, and dispersion. The mathematics of this optimization would be well worth exploring.

Comparison to Linear Measures of Searching Intensity

Several authors have quantified searching intensity in terms of the ratio of the beeline distance to the path length, which I will call the "beeline ratio," $R = B/L$ (Smith 1974; Zach & Falls 1977; Williamson & Gray 1975). A moment's reflection on the result of making a series of right turns followed by a set of left turns of similar magnitude, compared to that of alternating turns to the left and right, suggests that this measure is likely to depend strongly on the particular sequence of choices in the search path. As a consequence, the coefficient of variation of *B* in the hexagonal matrix model was about twice that of *D*. A less variable measure could be obtained from the ratio of the diameter of the circumscriptive circle to the path length, $P = D/L$. It is instructive to contrast the two linear ratios, *R* and *P*, and the

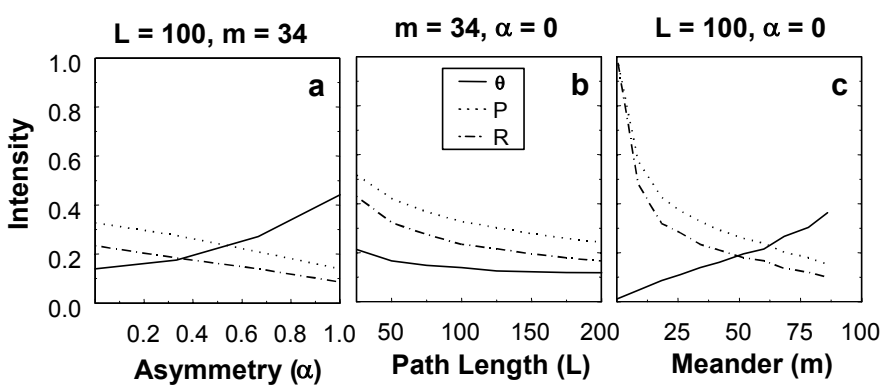

Figure 3. Three measures of searching intensity, R, P, and θ, contrasted at varying levels of asymmetry, path length, and meander**.**

areal measure, θ, with regard to their usefulness in characterizing a random searching pattern. An optimal measure of searching intensity should be relatively insensitive to variation in path length and should increase uniformly with increases in meander and asymmetry. Comparison curves are plotted in Fig 3a-c.

With $\alpha = 0$ and a moderate level of meander, θ is significantly less sensitive to changes in *L* than either *R* or *P* (Fig. 3b). Although the slopes of all three curves are greater at higher levels of *m* and α, the difference between them remains apparent. For meander, *R* and *P* consistently decrease with increasing *m* (Fig. 3c), counter-intuitively exhibiting higher searching intensities with less convoluted paths. The relationship between meander and *R* and *P* is also highly nonlinear, tending to exaggerate the effects of differences in meander at the lower end of the scale. This is, moreover, the worst case so far as θ is concerned. At higher levels of α, θ still remains roughly linear in *m*, while the nonlinearity of *R* and *P* is magnified. The three measures are fairly comparable in the regularity of their response to asymmetry (Fig. 3a), but the linear ratio measures show higher intensities for less asymmetrical paths, again contrary to the intuitive notion of intensive searching (Bond 1980). It appears that thoroughness should be preferable to a linear ratio as a characterizing variable for studies of random foraging, even when efficiency is not of particular interest.

Thoroughness in the Analysis of Empirical Data

If the data available are sufficiently detailed to allow estimation of meander and asymmetry, it is possible to test for the occurrence of systematic searching by application of the relations derived in the simulation. As an example of this technique, data from a study of the open-field searching behavior of larval green lacewings (Bond 1980) were reanalyzed to look for differences in the degree of randomness between successive phases of the search. In this study, the position of the animals was recorded in 1.5-sec steps before ("extensive phase"), during ("intensive phase") and after ("recovery phase") discovery and exploitation of a prey patch. To make the empirical measurements comparable to the results of the simulation, the data transcripts had to be converted to constant step lengths. The mean diameter of two contiguous hexagons perpendicular to a line connecting their centers is $S\sqrt{3}/2$, where *S* is the distance between the centers. We extracted steps of a constant length, about 1.15 times the average path width, from the path sequences by interpolation. Empirical values of thoroughness could be calculated for each path segment using Eqn. 4 and then compared to the Poisson expectation of a random search using Eqn. 6. The larger the disparity between these two estimates, the larger the systematic component in the search. Because *O* and *D* can take only integral values in the model, however, there is some hazard in attempting to generalize directly to the continuous case in this fashion.

Instead, we employed a more conservative approach that simply computed a multivariate regression of θ, as estimated from Eqn. 6, on *m* and α^2, reasoning that the regression coefficient should provide a direct indication of the degree of randomness of the search. Thoroughness, mean meander, and mean asymmetry were estimated for 318 twenty-step samples in the three search phases, and the regression of θ on *m* and α^2 was calculated for each phase. The coefficient was fairly high for the samples of extensive searching ($r = 0.79$, $N = 182$), suggesting little or no systematic avoidance of areas previously covered. It was somewhat reduced during intensive searching ($r = 0.69$, $N = 42$), though not significantly so ($p > 0.2$, using Fisher's Z-transformation), but the recovery phase correlation ($r = 0.44$, $N = 94$) was significantly lower than that from either of the other samples ($p < 0.05$), indicating a significant non-random component in the searching behavior. A subsequent autocorrelation analysis of signed turn magnitude in the recovery phase revealed a prominent trough between two and four lags that was not present in the spectrum from the extensive search data. This suggested that at least a portion of the reduced correlation was attributable to an increased tendency to alternate turn directions when moving away from a prey patch. That the thoroughness correlation was sensitive to this deviation from randomness is particularly gratifying, in that neither meander nor asymmetry alone was found to differ significantly, either in mean or in variance, between the extensive and recovery phases (Bond 1980).

Summary

The assumption that random, non-determinate searching behavior is less efficient than that resulting from a more structured and systematic strategy ignores the costs involved in specifying a systematic pattern and the potential flexibility of a random search when dealing with non-uniform resource distributions. To permit the assessment of the actual costs of random foraging, a simulation model was developed, and expressions were derived relating the thoroughness, dispersion, and degree of overlap of a random search to the parameters of the generating distribution. Several of these expressions were shown to lend themselves to characterization of empirical data and quantification of the occurrence of systematic components. More importantly, however, the derivations appear to offer an approach to the broader evolutionary questions of the relative costs and benefits of systematic foraging.

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