Optimal sinuosity in central place foraging movements

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Abstract. The case of a forager searching for immobile, randomly distributed prey items from a central place and homing straight back was examined to determine the optimal sinuosity of the search path. The optimal policy that was considered consists of minimizing the expected total (searching plus homeward) path length required to survey a given area, depending on the number of prey items the animal is able to load, its search path width and the prey density. The sinuosity of the search path must be low enough to minimize any overlapping between search path loops but high enough to minimize the homeward journey. Because of the complexity of the mathematical approach, the optimal sinuosity formula was derived using computer simulations. For a given prey density, the optimal sinuosity decreased logarithmically with the number of prey items the central place forager was searching for. The optimal sinuosity formula was also extended to deal with patchy environments. The applicability of this formula and its robustness to errors in the animal's estimate of the prey density are discussed.

Central place foraging provides an interesting case in the study of the movements of animals. An animal foraging from a central place has to take this spatial constraint into account in organizing its movements. The first theoretical study on central place foraging was carried out by Hamilton & Watt (1970), who investigated the resource partitioning between many individuals sharing the same central place, as occurs in the case of bird and social insect colonies. Numerous models predicting the optimal policy for central place foragers have been formulated in terms of search time (Andersson 1978), diet (Lessells & Stephens 1983; Houston & McNamara 1985), the load to be brought back to the central place (Kacelnik & Houston 1984), the sequence of patches to be visited (Ford 1983), the time spent in various patches (Green & Nunez 1986; Thomas 1988), the flight speed (Norberg 1981; Houston 1986), time and energy budgets (Houston 1987), and competition (Ydenberg et al. 1986). Studies of central place foraging have thus yielded important insights into optimal foraging theory (see reviews by Krebs et al. 1983 and Pyke 1984).

Only a few models have been developed, however, to determine the optimal path structure for a central place forager, although the optimal search path is one of the main concepts in the framework of this theory (Cody 1974; Pyke et al. 1977; Krebs 1978, 1979; Krebs et al. 1983; Pyke 1983, 1984; Benhamou & Bovet 1989). One exception is the model proposed by Morrison (1978), which deals with the case of an animal foraging for randomly distributed prey patches from a central place, to which it returns along a straight path as soon as it has harvested one prey item. The search path was represented by a simple random walk, i.e. by a sequence of steps and randomly distributed changes of direction, along which the animal forages with a given radius of detection. Morrison (1978) then attempted to determine the optimal ratio between the step length and the radius of detection, which minimizes the total (searching plus homeward) foraging time.

Because of the complexity of the arithmetical computations involved, Morrison (1978) took into account only the overlapping of one step with the previous one in determining the optimal ratio, but he neglected the growing possibility that the path might overlap with itself as the number of steps increases. Furthermore, as we have already pointed out (Bovet & Benhamou 1988), the simple random walk model does not accurately represent the movements of animals, because the cephalo-caudal polarization and the bilateral symmetry that are present in the majority of animals result in a...
tendency to go forwards that this model does not account for. In this previous paper, we developed a first-order correlated random walk model, which takes into account the forward tendency of the majority of animals, to compute the sinuosity of their paths. The concept of sinuosity was shown to be useful for analysing some space use and orientation mechanisms (Benhamou 1989; Benhamou & Bovet 1989; Benhamou et al. 1990; Bovet & Benhamou 1990). In the present study, we attempted to determine the optimal sinuosity of the random search path of a central place forager that brings a given amount of food back along a straight path. The model we developed deals with a forager such as an insect endowed with a basic spatial memory: it can memorize its home location but not the whole pattern of its ongoing search path. Consequently, it cannot systematically avoid previously surveyed portions of the area. One of us has carried out a preliminary approach to this problem (Bovet 1983).

THE MODEL

Let us consider a forager that returns to a central place along a straight path as soon as it has harvested a given amount of food. No foraging occurs during the homeward journey. The search path is represented by a first-order correlated random walk: it consists of a sequence of steps with length \( P \), and the changes of direction between successive steps are randomly drawn in a normal distribution with a null mean and a standard deviation \( \sigma \). The sinuosity, \( S \), of the search path, corresponding to the 'amount of turning' associated with a given path length, is then given by (Bovet & Benhamou 1988)

\[
S = \sigma / \sqrt{P}
\]

The animal is assumed to forage for pinpoint, randomly distributed prey items, using a search path width \( W \), until it has surveyed the area, \( A \)

\[
A = i/d
\]

where \( i \) is the whole number of prey items the animal brings back to the central place and \( d \) is the prey density. The prey items are assumed to be immobile and to be renewed only between two foraging bouts. The optimal policy then consists of minimizing the expected total (searching plus homeward) path length \( T \) required to survey area \( A \).

For this purpose, the animal during its search must on the one hand reduce the overlapping between loops of its ongoing search path, in order to avoid searching several times at the same place, and on the other hand, reduce its diffusion distance from the central place, which corresponds to the distance it will have to cover when it has finished searching. To fulfil the first requirement, the search path must have a low sinuosity, because the overlapping obviously increases with the sinuosity, whereas the second requirement means that the search path must have a high sinuosity, because the expected diffusion distance is inversely proportional to the sinuosity (Bovet & Benhamou 1988). There therefore exists an optimal sinuosity \( S^* \) taking these two antagonistic constraints into account, which minimizes the expected total path length. Since determining the value of this optimal sinuosity as a function of the area to be surveyed and the search path width is very difficult to handle arithmetically, we used computer simulations.

DETERMINING THE OPTIMAL SINUOSITY

We wished to find a relationship that gives the optimal sinuosity \( S^* \) as a function of the mean area to be surveyed \( A \) and the search path width \( W \). For this purpose, we attempted to determine the value of the standard deviation of the distribution of changes of direction \( \sigma^* \) that minimizes the expected total path length \( T \) with each of the following six values of the area to be surveyed: \( A = 50 W^2 \), \( A = 100 W^2 \), \( A = 200 W^2 \), \( A = 500 W^2 \), \( A = 1000 W^2 \) and \( A = 2000 W^2 \). Eight values of \( \sigma \), 0-25, 0-32, 0-40, 0-50, 0-63, 1-00 and 1-25 rad (i.e. 14°, 18°, 23°, 29°, 36°, 57° and 72°), were used. Only five consecutive values of \( \sigma \) were chosen, however, for each value of \( A \), so that the third value leads to the smallest total path length obtained (to standardize the polynomial estimation adjusting: see below). To estimate accurately the expected total path length required to survey a given area \( A \), 500 paths were simulated with a step length \( P \) equal to the search path width \( W \) \((P = W)\) for each value of \( \sigma \). The sinuosity of the paths is then given by \( S = \sigma / \sqrt{W} \).

Each path starts at the central place \((X_0 = 0, Y_0 = 0)\) and stops when area \( A \) has been surveyed. It is important to note that portions of area surveyed several times were taken into account only once,
because the prey items were assumed to be immobile and non-renewable during a foraging bout. From the technical point of view, the computation of the total length of each path was carried out by associating with it a 400 by 400 memory matrix. This matrix corresponds to equidistant points on the plane. It is reset to 0 at the start of the path, and a computer algorithm then gives the value 1 to all the matrix points that are less than $W/2$ units from the path during each step. When the total number of memory points equal to 1 reaches the limit corresponding to the area to be surveyed $A$, the number of steps $N$ and the coordinates $(X_N, Y_N)$ of the last point on the path are recorded. The total path length, $T = L + D$, is then computed from the search path length $L = NW$ and the homeward straight line path length $D = \sqrt{(X^2_N + Y^2_N)}$.

The average value of the 500 total path lengths was computed for each of the six values of $A$ and each of the five values of $\sigma$. With each value of $A$, a third degree polynomial function of $\sigma$ ($y = a + b \sigma + c \sigma^2 + d \sigma^3$) was adjusted to the five values of the mean total path length $T$ using the mean square method. With this type of function it was possible on the one hand to estimate reliably the mean total path length values obtained by simulation (Fig. 1), and on the other hand, to compute exactly the value $\sigma^*$ that minimizes this estimation for each value of $A$, by taking the derivative to be equal to 0 ($b + 2c \sigma^* + 3d \sigma^* = 0$) and solving the equation.

The value of $\sigma^*$ decreased approximately linearly with the logarithm of the ratio $A/W^2$. Then, using the mean square method, the most accurate estimate of the standard deviation of the distribution of changes of direction that minimizes the expected total path length required to survey a given area $A$ was computed as follows (Fig. 2):

$$\sigma^* = 1.20 - 0.11 \ln(A/W^2)$$

It should be recalled that the values of $\sigma^*$ were obtained from first-order correlated random walks with a step length $P$ equal to the search path width $W$. The general relationship is then deduced that expresses the value of the optimal sinuosity $S^*$ as a function of the area to be surveyed $A$ and the search path width $W$:

$$S^* = [1.20 + 0.11 \ln(dW^2)]/\sqrt{W}$$

**DISCUSSION**

The model proposed here predicts the optimal sinuosity of a search path depending on the amount of food a central place forager is searching for, its search path width, and the food density in the environment. This optimal sinuosity constitutes a compromise between an over-straight path which results in a lengthy homeward journey and an over-sinuous path which results in too much overlapping. The optimal sinuosity decreased with the area to be surveyed. There is no intuitive explanation for this function because of the complexity of the relationships between the amount of overlapping and the various characteristics (length, width and sinuosity) of the path. Before applying
Figure 2. Optimal standard deviation of the distribution of changes of direction as a function of the ratio between the area to be surveyed and the squared search path width. The dotted line indicates the most satisfactory estimation function we were able to obtain (see text).

In this model, it is necessary, however, to check some basic assumptions.

The search path is assumed to correspond to a first-order correlated random walk, whereas the homeward path is assumed to be rectilinear. On the one hand, it has been possible to model search paths as first-order correlated random walks in natural situations (Bovet & Benhamou 1988). On the other hand, accurate homing along a nearly straight path after a long sinuous search path seems to require an internal compass for memorizing the central place location by path-integration during the search path and for steering the homeward path (Benhamou et al. 1990). This kind of behavioural pattern appears to be common in some species of woodlice (Hoffmann 1984), beetles (Frantsevich et al. 1977), ants (Wehner & Wehner 1986), crickets (Beugnon & Campan 1989) and bees (Dyer & Seeley 1989) which are known to use a sun or a polarized skylight compass. For example, Serrastruma lujae ant search paths conform to a first-order correlated random walk, whereas their homeward paths approximate a straight line (Bovet et al. 1989).

The optimal policy we adopted in the model presented here consisted of minimizing the expected total (searching plus homeward) path length for a given area to be surveyed, i.e. for a given amount of food to be brought back to the central place. This policy ensures that the energy and time spent on each foraging bout are minimized when the speed and the cost per distance unit are the same for both the search path and the homeward path. Walking with a heavy load during the homeward journey can be much more expensive in terms of energy, however, than walking without any load and involves a slower speed. In addition, the distance to home can be biologically crucial because it is directly related to the time required to reach home should a predator be detected. Giving a greater weight to the distance to home in computing the total path length would result in a higher optimal sinuosity. On the other hand, an animal searching for cryptic prey items will move slowly during its search path to maintain a high probability of detecting prey items encountered (Gendron & Staddon 1983; Knoppien & Reddingius 1985). In this case, a greater weight should be given to the searching distance, which results in a lower optimal sinuosity.

The model presented here involves the assumption that the prey items are renewed only between successive foraging bouts. This assumption, which is commonly adopted in optimal foraging theory, seems to be fairly valid for many natural situations. Our model then implies the ability of the central place forager to estimate the prey density by sampling the environment. Fortunately, no very accurate estimate is required, because this model is quite robust to variations in the estimate of prey density. For example, consider a single-prey loader such as the small, nearly blind ant Serrastruma lujae. Its search path width can be estimated to be $W = 0.5$ cm. Let the prey density be $d = 40$ items/m$^2$ (0.004 items/cm$^2$); the ant has to survey an expected area $A = 250$ cm$^2$ $(1000 W^2)$. According to our model, the optimal sinuosity will then be 0.62 rad/cm$^{1/2}$. If the ant overestimates the prey density as 80 items/m$^2$ (twice the actual prey density), it will
forage with a sinuosity equal to 0.73 rad/cm$^{1/2}$, whereas if it underestimates the prey density as 20 items/m$^2$ (half the actual prey density), it will forage with a sinuosity equal to 0.51 rad/cm$^{1/2}$. It can be seen from Fig. 1 (curve $A = 1000 W^2$) that these poor estimates of the prey density entail only a very slight increase (less than 1%) in the expected total path length.

Maximizing the net rate of energy intake in the long-term is a fundamental principle of optimal foraging theory. In our model, the optimal sinuosity formula minimizes the total path length required to bring a given amount of food back to the central place. It is therefore of interest to determine how much food the animal must load at each foraging bout to maximize the long-term delivery rate of food to the central place. Our results have shown that the optimal policy consists of loading the maximum amount of food the animal is capable of (Fig. 1). For example, it is less expensive to survey a 2000 $W^2$ area in a single foraging bout (in this case, the minimal expected total path length is 2268 W) than in 40 foraging bouts each surveying a 50 $W^2$ area (in this case the minimal expected total path length is $40 \times 68 W = 2720 W$). These values correspond to a high prey renewal rate, renewal occurring after each foraging bout. Obviously, the advantage of taking a full load will increase as the renewal rate decreases.

The optimal sinuosity formula provided by this paper originally deals with homogeneous environments, where prey items are randomly distributed. It can be slightly modified to deal with heterogeneous environments, where prey items are aggregated in randomly distributed patches, which constitute a more realistic situation. In this type of environment, the animal has to search for patches in the same way as it searched for prey items in a homogeneous environment. For this purpose, the area to be surveyed must be rewritten as $A = i'/d'$, where $i'$ is the mean number of patches the central place forager has to visit to obtain a full load before returning home, and $d'$ is the patch density (mean number of patches per unit of area), and the search path width $W$ must be replaced by $W' = W + D$, where $D$ is the mean diameter of the patches. This revised optimal sinuosity formula obviously applies only to the search for patches: within a patch, the animal is likely to exhibit an area-concentrated searching behaviour by increasing its sinuosity (Benhamou & Bovet 1989), before resuming its random search for patches.

Lastly, it seemed to be worth comparing the efficiency of our probabilistic and realistic movement model with that of the most powerful, systematic but entirely hypothetical central place foraging movement model: the spiral. In this model, the animal is assumed to follow an Archimedes spiral centred on its central place during its search path, and to return in a straight line. It can be shown that the spiral model does not minimize the total path length needed for surveying a given area much more efficiently than the random search model: the expected total path length given by the latter model with an optimal sinuosity was only 17% longer on average than that given by the spiral model (see Fig. 1). This shows how efficient random movement searching can be.

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**REFERENCES**


Bovet, P., Dejean, A. & Granjon, M. 1989. Trajets d'approvisionnement à partir d'un nid central chez la


