Optimal Foraging: Movement Patterns of Bumblebees Between Inflorescences

GRAHAM H. PYKE*

Department of Biophysics and Theoretical Biology, The University of Chicago,
Chicago, Illinois 60637
Received June 21, 1977

Nectar-collecting bumblebees are hypothesized to employ rules of movement which result in the maximum net rate of energy gain (i.e., are optimal). The optimal movement rules are derived from a mathematical model and are used to generate predicted patterns of movement. The predicted patterns are compared with field observations. These observations support the hypothesis. An important component of the mathematical model is the memory of the foraging animal. The field data have implications concerning the memory capabilities of the bumblebees.

INTRODUCTION

Beginning with Emlen (1966) and MacArthur and Pianka (1966) and extending through the last 10 years several authors have sought to predict the foraging behavior of animals by means of mathematical models (e.g., Schoener, 1969, 1971; MacArthur, 1972; Charnov, 1973, 1976a, b; Pulliam, 1974; Maynard-Smith, 1974; Pyke, 1974, 1976a). All these authors assume that animals will forage in such a way that their fitness is maximized, and hence this approach to foraging behavior has become known as optimal foraging theory (Schoener, 1971; Charnov, 1973, 1976a, b; Pulliam, 1974). For detailed reviews of the literature on this subject the reader should consult Schoener (1971) and Pyke et al. (1977). The aim of the present study was to develop and test an optimal foraging model of bumblebee foraging behavior.

The system consisting of bumblebees and the plants they visit has many properties which make it ideal for a study of this kind. First, bumblebees fly fairly slowly between flowers and between plants and show no signs of disturbance when observed from distance as close as several inches. Hence their foraging behavior can be easily observed and quantitatively measured. Second, in the areas in which I have studied bumblebees (Colorado, Utah, and Arizona) there appear to be no predation on and no interactions between bumblebees while they are foraging. Furthermore, with the exception of male bumblebees

* Present address: Department of Biology, University of Utah, Salt Lake City, Utah 84112.
and seldom-seen virgin queens which may search for mates at the same time that they forage, foraging bumblebees are not searching for mates, nor are they searching for nest sites. At the beginning of a flowering season newly emerged queen bumblebees search for nest sites but this activity appears to be quite distinct from foraging. Hence, it is reasonable to hypothesize that the patterns evident in (nonmale) bumblebee foraging are adaptations solely for the obtaining of food. Third, while visiting many plant species bumblebees will restrict their activities to the collection of nectar. This nectar is taken back to the bumblebee's colony where it is stored and used as the source of energy for the colony. The growth, survival, and ultimate reproductive output of a colony should be strongly dependent on this stored nectar. Hence natural selection should have favored those bumblebees which maximize their net rate of energy gain while foraging for nectar. This leads to the following hypothesis which forms the basis for the present study: the patterns of behavior exhibited by bumblebees foraging for nectar are such that the net rate of energy gain is maximized. Such an energetic approach has been advocated for pollination biology in general by Heinrich and Raven (1972) and Heinrich (1975).

The particular aspect of bumblebee foraging that will be considered here is the pattern of movements of nectar-feeding bumblebees. So far only two authors have attempted to develop models to predict the movement patterns of animals (Cody, 1971, 1974; Pyke, 1974, 1976a) and all other discussions of the adaptive nature of movement patterns have been qualitative (e.g., Laing, 1937, 1938; Flanders, 1947; Dixon, 1959; Kaddou, 1960; Mitchell, 1963; Croze, 1970; Smith, 1971, 1974a, b; Tinbergen et al., 1967). Furthermore, animals may, in general, move for a variety of purposes, such as to obtain food, avoid predators, or find a mate. Hence, in general, movement patterns of animals will represent adaptations to this variety of factors, either separately or more likely in combination. In the present situation, however, it can be argued, as in the previous paragraph, that (nonmale) bumblebees are doing nothing except forage as they move amongst the flowers upon which they feed. Thus this bumblebee-plant system permits consideration of the adaptive nature of movement patterns in a pure foraging situation. Hopefully, the other kinds of movement mentioned above will receive attention in the future.

The hypothesis that will be tested below has now been slightly transformed into the following: during those times when bumblebees appear to be devoting all their time to the collection of nectar their movement patterns will be such that their net rate of energy intake is maximized. I shall discuss this hypothesis by first presenting a model of bumblebee movements from which are derived a number of properties of the movement pattern which maximizes the net rate of energy intake (i.e., the optimal movement pattern), and then presenting field observations on the equivalent properties of nectar-collecting bumblebees. Predicted optimal movement patterns and observed movement patterns correspond closely.
Methods

Field observations for this study were carried out on clear, windless days between June 25 and July 25, 1972, in a subalpine meadow near the Rocky Mountain Biological Laboratory, Crested Butte, Colorado, at an elevation of 9500 feet. Most observations were made at the center of a large, dense patch of monkshood, *Aconitum columbianum*, but some observations were also made in an area of larkspur, *Delphinium nelsoni*. The most numerous animals foraging among the *Aconitum* and *Delphinium* flowers were nectar-collecting workers of the bumblebee species, *Bombus flavifrons* and queens of *Bombus appositus*, respectively, and observations were restricted to these individuals.

Flowers of both plant species occur on vertical inflorescences and these inflorescences form large two-dimensional arrays. Directions of movements between inflorescences were recorded relative to the direction of the previous movement using the same method as that used by Levin *et al.* (1971). This consists of assigning the direction of a movement relative to the previous movement to one of eight compass directions (N, NE, E, etc.) where N represents "straight ahead" or "in the same direction as the previous movement," etc. Distances moved between inflorescences and the number of flowers visited per inflorescence were also recorded.

Directions and distances of movement between inflorescences and the number of flowers visited/inflorescence describe movement patterns of foraging bumblebees fairly completely. The following model will ultimately be concerned with properties of this description of movements.

The Model

To formulate a model of movements of an animal while it searches for food it is necessary to make a number of assumptions concerning the spatial and temporal distribution of food and the rules and constraints governing the movements of the animal. It will be assumed, for example, that all gains and costs involved in movements can be expressed in units of energy. The aim of the following model is to determine the rules of movement, which, subject to the various constraints, maximize the overall net rate of energy gain by an animal. This will be referred to as the "optimal" movement pattern and the parameters of this movement pattern will be termed "optimal."

The following assumptions are made concerning the distribution of food. They are expressed in a fairly general form but, in this study, they are specifically intended to be realistic assumptions in the case of animals collecting nectar or pollen from plants which grow in meadow-like situations.

1. Food occurs only at discrete resource points (e.g., flowers or clusters
of flowers) and an animal does not "know" how much food is at a resource point until it moves to that point and removes what food is there.

(2) The food is nonrenewable during a single foraging bout of an animal but is renewable between foraging bouts. This assumption is made in order to keep the mathematics relatively simple.

(3) Resource points occur in a fairly dense two-dimensional array (e.g., flowers in a meadow or field) and this array does not change over time.

(4) Resource points cover a large area, so that it is very rare for an animal to encounter the boundary of the resource points.

(5) The gain to an animal from obtaining the food may be represented in terms of energy units/unit of food. This seems particularly reasonable in the case when the food is nectar, which is the principal source of energy to a number of animals.

The following additional assumptions are made concerning the movements of the animals. They are likely to represent a good approximation to the way in which many flower-visiting animals move between flowers and clusters of flowers.

(6) The foraging bouts of the animals are long, i.e., many resource points are visited.

(7) Several similar animals are foraging among the resource points and there is some overlap of the foraging areas of the animals.

(8) When leaving a resource point and "choosing" the next, an animal may make use of various pieces of information. The animal may "known," for example, the direction of arrival at the resource point and/or the amount of food obtained from the resource point. An animal with only such knowledge can be considered to have a short memory. The animal may also know the directions of arrival and/or the amounts of food obtained at previous resource points. The greater the number of previous resource points about which the animal has information, the longer is its memory. The model will be developed and tested below in terms of these different levels of memory.

(9) Animals move from one resource point to another by "aiming" the departure from a resource point in some direction relative to the arrival direction, visually "scanning" a sector of a certain angular width about the aimed direction, and moving directly or linearly to the closest point within that sector (Fig. 1). The choices of the aimed departure direction and the size of the scanning sector are assumed to be made independently of one another.

The rule of movement defined by assumptions 6–9 seems reasonable for the following reasons:
76 GRAHAM H. PYKE

Fig. 1. After reaching the resource point $P$, the animal aims its direction of departure from $P$ in the direction $a$, then visually scans the shaded sector of angular width $w$ and finally moves to the closest resource point within this sector. The direction of arrival at $P$ is indicated by $c$, the direction of actual departure from $P$ is indicated by $b$, and $\theta$ is the actual change in direction at the resource point $P$.

(1) An animal's choice of the next resource point to visit will most likely depend on the directions and distances to the various possible resource points.

(2) For direction to be important there must be a reference direction and the best candidate for this is the direction of arrival at the resource point.

(3) In terms of foraging efficiency, an animal does best by moving to the closest of all the resource points lying in any one direction. Hence an animal is likely to choose the closest resource point subject to certain directional constraints.

(4) Bees and hummingbirds, when flying between flowers and between clusters of flowers, appear to do so in a direct or linear fashion so long as the density of flowers is not too low and visibility is reasonably good (personal observations). Hence, in general, animals are assumed to move between resource points that are visible from one another do so in a direct linear manner.

The above rule of movement introduces the following variables which will all feature in the development of the model (see Fig. 1):

(i) The angular difference between the aimed direction (Direction "a" of Fig. 1) of departure from a resource point and the direction ("c") of arrival at the resource point. If clockwise differences are taken as positive and counterclockwise differences as negative, the frequency distribution of this angle will be defined on $(-\pi, +\pi)$.

(ii) The angular width $w$ of the scanning sector. In this case $0 \leq w \leq 2\pi$. 
(iii) The angular difference between the aimed ("a") and actual ("b")
departure directions. As in (i) above the frequency distribution of this angle
will be defined on \((-\pi, +\pi)\).

(iv) The angular difference \(\theta\) between the directions of arrival at ("c")
and actual departure from ("b") a resource point. The frequency distribution
of \(\theta\) will also be defined on \((-\pi, +\pi)\).

(v) The distance moved from one resource point to the next. Only the
last two of these variables can, however, be measured in the field and the
following model will concentrate on developing predictions in terms of them.
These variables may, as mentioned in (6) above, depend upon the array of
information available to the animal.

Before proceeding with the development of the model the following parameters
must be defined and an additional assumption must be made.

(a) Let \(X_1\) be the energetic cost to an animal/unit time of moving between
resource points and let \(X_2\) be the energetic cost to an animal/unit time during
the time spent at the resource points. I shall assume that \(X_1 \geq X_2\), though this
may not be true for hummingbirds or other animals which hover while feeding
at flowers.

(b) Suppose that \(t(x) = c_1 + c_2 \cdot x\) is the time spent by an animal in
obtaining \(x\) units of energy from a resource point. \(c_1\) is the time involved in
landing, while \(1/c_2\) is the actual rate of extraction of energy from the resource
point, and so \(c_1, c_2 > 0\).

(c) Let \(v\) be the speed of movement between resource points.

(d) Let \(\bar{e}\) be the mean amount of energy obtained by an animal/resource
point and let \(\bar{d}\) be the mean distance moved between successive resource
points.

An expression for the overall net rate of energy gain can now be derived as
follows:

1. The mean net energy gain/resource point \((G)\) is equal to the mean
energy obtained/resource point less the mean cost of movement between
resource points and less the mean cost of spending time at each resource point;
i.e.,

\[
G = \bar{e} - X_1 \cdot \bar{d}/v - X_2 \cdot (c_1 + c_2 \cdot \bar{e}).
\]

2. The mean time taken/resource point \((T)\) is the sum of the mean time
spent moving between resource points and the mean time spent at each resource
point; i.e.,

\[
T = \bar{d}/v + (c_1 + c_2 \cdot \bar{e}).
\]
(3) Since the foraging bout is long (assumption 6), the mean overall net rate of energy gain \( E \) is equal to \( G/T \); i.e.,

\[
E = \frac{\bar{e} - \lambda_1 \cdot \bar{d}/v - \lambda_2 \cdot (c_1 + c_2 \cdot \bar{e})}{d/v + (c_1 + c_2 \cdot \bar{e})}.
\]

This net rate of energy gain \( E \) is actually a function of the rules of movement by virtue of the fact that both \( \bar{d} \) and \( \bar{e} \) depend on these rules. Furthermore, this rate is a function of the information that an animal is assumed to use (i.e., of the animal's assumed memory level) since \( \bar{d} \) and \( \bar{e} \) are also functions of this information. Hence the movement rules that maximize \( E \) (i.e., the optimal movement rules) will depend on the animal's assumed memory level. For this reason the various memory levels will be considered separately in the following development of the model. For each memory level optimal rules of movement will be determined, compared with the optimal rules for other levels and compared with the available data.

**Memory level 1.** No knowledge of any movement directions.

If an animal has no knowledge of any movement directions then the direction of aimed departure from a resource point will be independent of the direction of arrival at the resource point and hence there will be a uniform distribution of aimed departure directions (i.e., all directions equally likely). Since the actual departure direction depends only on the aimed departure direction and the sector width employed at the resource point, there will also be a uniform distribution of actual departure directions. In other words, the animal should move randomly amongst the array of resource points (Pyke, 1976a).

Distributions of actual departure directions for bumblebees moving between inflorescences of *Delphinium nelsoni* and *Aconitum columbianum* were, however, far from uniform relative to the directions of arrival at the inflorescences (Figs. 2a and 2b). In fact the distribution of the differences between departure and arrival directions was unimodal with a fairly low variance and a mean of approximately 0° (see Figs. 2a and 2b). In other words, the departures from inflorescences tended strongly to be in the same directions as the arrivals at the inflorescences. This could only be true if the bumblebees' memory included a knowledge of the directions of arrival at the inflorescences or if the bumblebees tended to maintain a constant compass direction. The latter was clearly not the case, however, because bumblebees that were tracked were found to vary greatly the general direction of their paths over very short periods of time and the occasional reversal of direction was not followed by an immediate compensatory reversal (see Conclusions). The recorded movements were not affected by wind (see Methods). Hence, bumblebees have a knowledge of the directions of arrival at inflorescences and tend to maintain the same direction when departing from the inflorescences. Such a tendency has also been found to
Fig. 2. The frequency distribution of changes in direction at inflorescences (i.e., of the direction of actual departure from an inflorescence minus the direction of arrival at the inflorescence) is shown for movements of workers of Bombus flavifrons (a) and queens of Bombus appositus (b) between inflorescences of Aconitum columbianum and Delphinium nelsoni, respectively. The mean angles are $-3.4$ and $0.3^\circ$, respectively, and neither of these differs significantly from $0^\circ$.

Hold for bees and butterflies visiting flowers of Lythrum salicaria (Levin et al., 1971).

Memory level 2. Knowledge only of the direction of arrival at the present resource point.

If an animal has knowledge only of the direction of arrival at the present resource point then the mean distance $d$ moved to the next resource point will be a function simply of the angular width $w$ of the scanning sector. Furthermore, if the resource points are distributed at random in space (i.e., two-dimensional Poisson distribution), then the mean distance $d$ to the next resource point is given by:

$$d(w) = c/w^{1/2}\rho^{3/2}$$

where $c = (\pi/2)^{1/2}$ and $\rho$ is the density of resource points.

However, even if resource points are not distributed at random, $d(w)$ should equal $d(w)/\rho^{1/2}$ where $d(w)$ is a function of very similar shape to $c/w^{1/2}$. Hence, I shall assume that

$$d(w) = d(w)/\rho^{1/2}$$

where $d(w)$ is the mean distance to the next resource point when a sector of width $w$ is employed and $d(w)$ has the following properties:

$$d'(w) < 0 \quad \text{for all } w,$$
$$d(w) \to \infty \quad \text{as } w \to 0,$$
$$d''(w) > 0 \quad \text{for all } w.$$
This formulation for $d(w)$ will be used in a later section. For the present it is sufficient to note that $d$ is a function of $w$ and not of any of the other variables which arose earlier from the assumptions about the rules of movement.

Whatever the level of memory the mean amount of energy ($\bar{e}$) obtained by an animal per resource point will depend primarily on the frequency with which resource points are revisited by the animal. In fact, $\bar{e}$ is given by

$$\bar{e} = (1 - f) \cdot \bar{x}$$  \hspace{1cm} (4)$$

where $f$ is the proportion of resource points on the path of the animal that are revisits and $\bar{x}$ is the mean amount of energy present in unvisited resource points. By assumption 2, no energy is obtained from a revisited resource point. This frequency of revisitation will depend, in turn, on the rules of movement (Pyke, 1976a). Hence, before proceeding, it is necessary to consider this relationship between the rules of movement and the frequency with which resource points will be revisited.

Pyke (1976a) has shown that if the resource points are arranged in a regular lattice, if the array of resource points is very large, but bounded, and if the directions of a movement depend only on the direction of the previous movement, then the frequency with which an animal revisits resource points decreases as the correlation between the directions of successive movements increases, except when the correlation is very nearly equal to 1. This last qualification is not required if the array of resource points has essentially infinite size (Pyke, 1976a). In other words, the stronger the tendency of an animal to maintain a straight line course, the lower is the frequency of revisiting resource points, except when the animal's path becomes extremely close to being perfectly linear. Although the resource points in the present model are not so regularly distributed, I shall make the assumption that the same result holds for the distributions of resource points encountered in nature. Hence, the frequency of revisitation with the present level of memory will decrease with increases in the correlation between the directions of arrival at and departure from the resource points.

Since the choices of aimed and actual departure directions are assumed to be carried out independently of one another (assumption 9), this correlation between the arrival and departure directions is simply the product of two other correlations, namely, that between the arrival direction and the aimed departure direction and that between the aimed departure direction and the actual departure direction. Hence, the frequency of revisitation will in the present situation decrease as the product of these two correlations increases.

The correlation between the arrival and aimed departure directions depends solely on the relationship between these two directions and is clearly maximal when the two directions are identical (i.e., correlation is 1). On the other hand, the correlation between the aimed and actual departure directions is, like the mean distance to the next resource point, a function solely of the angular width
of the sector and the distribution of resource points. This correlation will clearly increase as \( w \) decreases. Hence the frequency of revisitation is minimized, independent of the size of \( w \), when the arrival and aimed departure directions are identical and is an increasing function of the angular width \( w \) of the scanning sector.

The mean overall net rate of energy gain \( (E) \) is maximized, independent of the size of \( w \), when the arrival and aimed departure directions are identical. For, if Eqs. (1), (2), and (4) are combined and \( E \) is differentiated with respect to \( f \), then

\[
\frac{\partial E}{\partial f} = \frac{w}{\{d/v + (c_1 + c_2 \cdot \delta)\}^2} \cdot \{-c_1 - d/v(c_2(\lambda_1 - \lambda_2) + 1)\}
\]

\[
< 0 \quad \text{since} \quad \lambda_1 \geq \lambda_2.
\]

Hence \( E \) is maximized when \( f \) is minimized, assuming \( w \) is constant, and \( f \) is minimized when the arrival and aimed departure directions are identical. The optimal \( w \) now remains to be considered.

At present the size of the optimal angular sector width \( \omega \) cannot be determined, but it almost surely must lie within the range \( 0 < \omega < 2\pi \) and must not be at either extreme point of the range. For as \( w \) increases in magnitude there is a trade-off between the advantage of a decreasing average distance between resource points (see Eqs. (2) and (3)) and the disadvantage of an increasing frequency of revisitation (see Eq. (9) and the argument following it). The optimum certainly could not be \( 0^\circ \) since this would result in infinitely large distance between successive resource points. Furthermore, it could not be \( 2\pi \) because employment of such a sector width would quickly lead to the animal's path consisting of only a few close resource points between both of which the animal would move indefinitely. The number of resource points in this "infinite loop" would be 3 if the animal were able to avoid its arrival direction and would be 2 if it were not. Hence the trade-off will result in some intermediate value for the optimal \( w \). The exact value for this optimum can be determined only when quantitative estimates are available for the various parameters and functions which appear in the equations.

In summary, when the animal has knowledge only of the directions of arrival at the resource points, it should always aim its departure from a resource point in the same direction as that of arrival and should employ a scanning sector of angular width \( \omega \) where \( \omega \) has a value intermediate between \( 0^\circ \) and \( 2\pi \). This conclusion leads to the following two predictions:

(i) Within the angular width \( w \) all directions for the next resource point will be equally likely. Hence the frequency distribution of \( \theta \), the angular difference between the arrival and actual departure directions, should be uniform (between \(-\omega/2\) and \(+\omega/2\) and should have a mean of \( 0^\circ \).
For a scanning sector of angular width \( w \) and a random distribution of resource points, the frequency distribution of \( d \) is given by the above equation which is the equation for a strongly leptokurtic distribution (i.e., frequencies of both short and long movements greater than those expected from a normal distribution). Hence, the frequency distribution of \( d \), the distance between successive resource points, should be strongly leptokurtic. As argued above, the actual frequency distribution of \( d \) should be similar, at least in shape, to this distribution even if the resource points are not distributed at random.

The first of these predictions is fulfilled in part. As mentioned above the means of the frequency distribution of \( \theta \) for bumblebees visiting *Delphinium nelsoni* and *Aconitum columbianum* were found to be close to 0° (Figs. 2a and 2b) and the means for bees and butterflies visiting were found by Levin et al. (1971) to be close to 0°. In all these cases the differences from 0° are not significant at the 5% level (Student's \( t \) test). However, the frequency distributions in all these cases were far from being uniform (see Figs. 2a, 2b). A possible explanation for this is that the bumblebees employ different sector widths depending on the circumstances. In fact, if the sector width \( w \) has some frequency distribution, then whatever the frequency distribution of \( w \), the frequency distribution of \( \theta \) will be unimodal and symmetric and have a mean of 0°. This possibility of a variety of sector widths will be discussed in the next section.

The second of these predictions is also supported by the available data. The distribution of distances moved by workers of *Bombus flavifrons* between successive inflorescences of *Aconitum columbianum* is shown in Fig. 3. This distribution is clearly strongly leptokurtic, as predicted. Similar leptokurtic distributions have been found for movements of andrenid bees and honeybees (Bateman, 1947a, b), bumblebees (Bateman, 1947b, c), butterflies (Levin and Kerster, 1968), and bees (Levin and Kerster, 1969a, b).

![Fig. 3. The frequency distribution of distances flown by workers of *Bombus flavifrons* between successive inflorescences of *Aconitum columbianum.*](image-url)
Memory level 3. Knowledge of the direction of arrival at the present resource point and the amount of energy obtained from the present resource point.

That bumblebees (present study) and bees and butterflies (Levin et al., 1971) must have a knowledge of the direction of arrival at a flower or cluster of flowers is shown by the strong tendency for the departure and arrival directions to be identical. The most likely information for them to also have at the same time is a knowledge of the amount of energy just obtained. Hence the next logical level of memory is where the animal has a knowledge of both the direction of arrival at and the amount of energy obtained from the present resource point.

If an animal has knowledge of the amount of energy obtained at a resource point then it could vary the angular width of the scanning sector as a function of this amount of energy obtained. This would seem to be a likely possibility and it would, as argued above, potentially explain the observed frequency distribution of \( \theta \), the difference between the arrival and departure directions. I now assume that the animal does in fact vary the sector width as a function of the amount of energy obtained at a resource point and I shall investigate the consequences of this assumption.

Before proceeding the following parameters must be defined:

(a) The amount of food (energy) in unvisited resource points is probably a continuous random variable (certainly in the case of nectar). As a discrete approximation to the frequency distribution of this random variable, suppose that the proportion of unvisited resource points which contain \( x_i \) units of energy is \( 1/n \) for all values of \( i \) where \( i = 1, \ldots, n \) and \( x_{i+1} > x_i \). This somewhat unusual way of making such an approximation is chosen to prevent later mathematical difficulties. Also let \( x^0 \) be the amount of energy obtained during a revisit to a resource point. Then, by assumption 2, \( x^0 = 0 \).

(b) Similarly, suppose that, when an animal obtains \( x_i \) units of energy at a resource point, it employs, in choosing the next resource point, a sector of angular width \( w_i \) where \( i = 0, 1, \ldots, n \).

(c) Let \( e_i = \) the mean energy obtained at the next resource point if the amount of energy obtained at the present resource point is \( x_i \) (i = 0, 1, ..., n).

Simple equations for \( d \) and \( \bar{d} \) can now be established. First, since the overall mean distance between resource points (\( d \)) is simply equal to the proportion \( (1 - f) \) of resources points which are not revisits multiplied by \( (1/n) \sum_{i=1}^n d(w_i)/\rho^{1/2} \), which is the mean distance from such a resource point to other resource points, plus the proportion \( f \) of revisits multiplied by the mean distance \( d(w^0)/\rho^{1/2} \) from a revisited resource point to another, \( d \) is given by

\[
d = \frac{(1 - f)}{n \rho^{1/2}} \sum_{i=1}^n d(w_i) + \frac{f}{\rho^{1/2}} d(w^0). \quad (6)
\]
Similarly, $\epsilon$ is given by

$$\epsilon = \frac{(1 - f)}{n} \sum_{i=1}^{n} e_i + f \cdot e_0 \quad (7)$$

where expressions for the $\{e_i\}$ are yet to be determined.

Some properties of $f$, the proportion of revisits to resource points, can also be determined. First, it will be recalled that $f$ decreases as the correlation between the arrival and departure directions increases and that this correlation is the product of the correlation between the arrival and aimed departure directions and that between the aimed and actual departure directions. Hence, $f$ can be written as

$$f = f(g \cdot h) \quad (8)$$

where $g$ is the correlation between the arrival and aimed departure directions, $h$ is the correlation between the aimed and actual departure directions, and

$$\frac{\partial f}{\partial (gh)} < 0. \quad (9)$$

Second, the correlation ($h$) between the aimed and actual departure directions will be a function of the sector widths $\{w_i\}$ (i.e., $h = h(w_0, w_1, \ldots, w_n)$) and will clearly satisfy the relation

$$\frac{\partial h}{\partial w_i} < 0 \quad \text{for all } i; \quad (10)$$

i.e., the correlation decreases as any one of the sector widths increases. Third, since any two sector widths $w_i$ and $w_j$ occur equally often (since $x_i$ and $x_j$ occur equally often),

$$\frac{\partial h}{\partial w_i} = \frac{\partial h}{\partial w_j} \quad \text{if } w_i = w_j. \quad (11)$$

Finally, if the relations (8), (9), and (10) are combined the following set of results is obtained:

$$f = f(g \cdot h(w_0, w_1, \ldots, w_n));$$

$$\frac{\partial f}{\partial g} = 0;$$

$$\frac{\partial f}{\partial h} < 0; \quad (12)$$

$$\frac{\partial f}{\partial w_i} > 0 \quad \text{for all } i;$$

$$\frac{\partial f}{\partial w_i} = \frac{\partial f}{\partial w_j} \quad \text{if } w_i = w_j;$$

i.e., the frequency of revisitation increases as the correlation between the arrival and aimed departure directions decreases and also increases as any one of the scanning sector widths increases.
An expression is still needed for $e_i$ as a function of the movement rules. The way to obtain such an expression is suggested by the following consideration of the factors responsible for the distribution of energy availabilities in resource points not yet visited by the animal.

(1) The amount of energy at a resource point depends on the production rate of this energy and the time since the point was last visited by an animal during a previous foraging bout. The shorter this time the lower the amount of energy available at the resource point.

(2) During a foraging bout an animal will revisit resource points on its own path and will also visit resource points on the previous paths of other animals (assumption 7). When the animal has just visited such a resource point on a previous path, there will then be a certain probability that the next resource point visited by the animal will lie on the same previous path. This would become increasingly disadvantageous as the amount of energy obtained at the first resource point decreases (i.e., as the previous path becomes more recent) since, the more recent a previous path is, the lower will be the average amount of energy in other resource points along the same path.

(3) The probability that the animal will move from a resource point to another on the same previous path should increase as the width of the sector employed at the first resource point increases. Hence the optimal strategy might be to employ a sector width which increases as the amount of energy obtained increases. I shall now consider this possibility in a more detailed and rigorous manner.

Let $P(w)$ be the probability that, having just visited a resource point on a previous pathway, an animal will then move to another resource point on the same pathway if it employs a scanning sector of angular width $w$. This probability is then the product of the probability $P_1(w)$ that a resource point on the previous pathway is included in the area scanned by the animal and the conditional probability $P_2(w)$ that this resource point on the previous pathway is actually the closest resource point in the animal's scanning area. The first of these two probabilities, $P_1(w)$, will increase steadily from 0 to 1 as $w$ increases from 0 to $2\pi$ while the second probability, $P_2(w)$, takes the value 1 when $w$ is 0 and decreases as $w$ increases. This decrease will, however, be slight since the animal that created the pathway will have moved from one resource point to another that is the closest within some sector that starts at the resource point. $P(w)$ will therefore be an increasing function of $w$ when $w$ is less than some value $W$ and will be a decreasing function of $w$ when $w$ is greater than $W$; i.e.,

$$P'(w) > 0 \quad \text{for } w < W,$$

$$P'(w) < 0 \quad \text{for } w > W.$$
Suppose that a resource point contains \( x \) units of energy. Then unless \( x \) is the maximum possible \( (x(\text{max})) \), this resource point will lie on the previous pathway of an animal. Let \( r(x) \) be the mean amount of energy at another resource point on this previous pathway if this resource point has not been already visited by the animal whose foraging bout is being considered. Then \( r(x) \) will increase from 0 to \( \bar{x} = \sum_{i=1}^{n} x_i/n \) as \( x \) increases from 0 to \( x(\text{max}) \); i.e.,

\[
\begin{align*}
    r(0) &= 0, \\
    r'(x) &= 0, \quad \text{as} \quad x \to x(\text{max}); \\
    r(x) &\to \bar{x} \quad \text{as} \quad x \to x(\text{max});
\end{align*}
\]

where

\[
\bar{x} = \sum_{i=1}^{n} x_i/n.
\]

An expression for \( e_i \), the mean energy obtained at the next resource point if the amount of energy obtained at the present resource point is \( x_i \), can now be determined. If the animal obtains \( x_i \) units of energy at a resource point, the mean amount of energy that it obtains from the next resource point will be \((1 - f) \cdot r(x_i)\) if it moves to a resource point in the same previous pathway and \((1 - f) \sum_{i=1}^{n} x_i/n\) if it does not. Combining these with the definition of \( P(w) \) leads to the following:

\[
e_i = (1 - f) \cdot r(x_i) P(w_i) + (1 - f) \sum_{i=1}^{n} x_i/n \cdot (1 - P(w_i)).
\]

If Eqs. (1), (2), (3), (6), (7), (12), and (15) are all combined it is now seen that \( E \) is a function of the sector widths \( \{w_i\} \) and of the correlation \( g \) between the arrival and aimed departure directions, i.e., \( E \) is determined by the rules of movement. The next step is then to determine the movement rules which, for this memory level, maximize \( E \). It will be seen that the optimal sector widths do, as suggested by intuition, increase with increasing amounts of energy obtained per resource point and that the optimal correlation between the arrival and aimed departure directions is 1.

The following result is obtained if Eqs. (1), (2), (3), (6), (7), (12), (13), (14), and (15) are combined and then \( \partial E/\partial w_i \) is determined:

\[
\begin{align*}
    (\partial E/\partial w_{i+1}) - (\partial E/\partial w_i) &> 0 \quad \text{when} \quad w < W \\
    (\partial E/\partial w_{i+1}) - (\partial E/\partial w_i) &< 0 \quad \text{when} \quad w > W
\end{align*}
\]

for all \( i \), when \( w_j = \hat{w}_j \) the optimal \( w_j \) for all \( j \neq i, i + 1 \), and \( w_i = w_{i+1} = w \).
From this and Eq. (3) the following result is also obtained:

\[ \tilde{w}_{i+1} > \tilde{w}_i, \quad i \geq 0; \]
\[ \tilde{w}_i < W, \quad i \geq 0; \]
\[ \tilde{w}_i \to V \quad \text{as} \quad i \to n; \]  \hspace{1cm} (17)

where \( W \) is the sector width that gives the maximum probability that an animal will move from one resource point to another on the same previous pathway, and \( V \) is some sector width less than \( W \). In other words, the optimal sector widths \( \tilde{w}_i \) increase with increasing values of \( x_i \) and reach an asymptote of \( V \approx W \).

If Eqs. (1), (2), (3), (6), (7), (12), and (15) are combined and \( \partial E/\partial \phi \) is determined, then

\[ \partial E/\partial \phi > 0 \quad \text{for all} \quad \phi \]  \hspace{1cm} (18)

where \( \phi \) is the correlation between the arrival and aimed departure directions. Hence \( E \) is maximized when this correlation takes its maximum value of 1. In other words, the animal should always aim its departure from a resource point in the same direction as that of arrival at the resource point. It should then employ a sector width which increases in size as the amount of energy obtained at the resource point increases.

Before proceeding, some statistical terminology used to describe circular distributions must be introduced. Statistics for circular distributions have been presented in summary form by Batschelet (1965) and I shall adopt the same terminology that he uses. The most useful statistics for describing these distributions are the mean angle and the mean angular deviation. These are analogous to and have similar properties to the familiar mean and standard deviation, respectively (Batschelet, 1965) (i.e., the mean angular deviation is a measure of the “width” or “spread” of a circular frequency distribution).

Some predictions can now be derived in terms of the frequency distribution of the difference between the arrival and departure directions and the distribution of distances moved between successive resource points.

(1) The frequency distribution of the angular difference between the arrival and departure directions should be a unimodal, symmetric distribution with a mean angle of 0°. Since the arrived and aimed departure directions are predicted to be identical, the frequency distribution of this angular difference \( \theta \) between the arrival and departure directions should be uniform on the interval \((-\tilde{\phi}/2, +\tilde{\phi}/2)\) for each sector width \( \tilde{\phi} \). Such a uniform distribution has a mean angle of 0°. Further, since the optimal sector width \( \tilde{\phi} \) has itself a frequency distribution, the overall frequency distribution of \( \theta \) should be a composite of all the separate uniform distributions corresponding to each \( \tilde{\phi} \). The frequency distribution of \( \theta \) should thus be unimodal, symmetric, and have a mean angle of 0°. (See the previous section.)
This prediction is borne out well by available data. In Figs. 2a and 2b frequency distributions of the direction of (actual) departure from an inflorescence minus the direction of arrival at the inflorescence (θ) are shown for movements of workers of Bombus flavifrons and queens of Bombus appositus between inflorescences of Aconitum columbianum and Delphinium nelsoni, respectively. In both cases the distributions are unimodal, appear to be symmetric, and have mean angles which do not differ significantly from 0° at the 5% level (Student's t test). These properties also hold for the movements of bees and butterflies between flowers of Lythrum salicaria (Levin et al., 1971).

(2) Just as in the case of the previous memory level, the frequency distribution of the distances between successive resource points should be strongly leptokurtic. For each sector width w and a random distribution of resource points, the distribution of distances should be given by \( F(d) = \rho d \exp(-\rho d^2/2) = \gamma d \exp(-\gamma d^2/2) \). The overall frequency distribution will be a composite of the separate distributions corresponding to each sector width and hence should be similar in shape to the distribution given by the latter expression. As mentioned in the previous section this prediction is also borne out by the available data.

(3) The mean angular deviation of the frequency distribution of \( \theta \), the difference between the arrival and departure directions, should increase as the amount of energy obtained at the resource point increases. For each sector width \( w \) the optimal distribution of \( \theta \) is uniform on the interval \((-w/2, +w/2)\) and such a distribution has a mean angular distribution \( S \) which is given by \( S = (2(1 - r))^{1/2} \) where \( r = 2 \cdot (\sin w/2)/w \) (see Batschelet, 1965). The mean angular deviation of the distribution of \( \theta \) therefore increases as \( w \) increases and hence that the optimal mean angular deviation increases as the amount of energy obtained at a resource point increases (see Eq. (17)). Furthermore, as the amount of energy obtained at a resource point increases, the mean angular deviation of the distribution of \( \theta \) should eventually reach an asymptote (see Eq. (17)).

Since this prediction and the next both involve the amount of energy obtained at a resource point, they cannot be tested without an estimate of this energy obtained. In the case of bumblebees and inflorescences this energy comes from the nectar in the flowers. However, it is not possible in the field to measure directly the amount of nectar obtained by a foraging bumblebee at each inflorescence. So an indirect measure of this amount is required.

As such an indirect estimate of the amount of nectar and hence energy obtained by a bumblebee at an inflorescence I shall use the number of flowers that the bumblebee visits on the inflorescence before leaving it. This estimate is satisfactory for the following reasons. For one of the species of bumblebees (B. appositus) and one of the plant species (A. columbianum) in this study, I have found that the more time a bumblebee spends at a flower or an inflorescence,
the more likely it is to fly to another flower on that inflorescence (Pyke, unpublished data). Since the amount of time that a bumblebee spends at a flower is an increasing function of the amount of nectar it obtains from the flower (Pyke, unpublished data), the above result suggests that the likelihood of a bumblebee flying from one flower to another on the same inflorescence increases with the amount of nectar obtained at the first flower. Hence the more flowers that a bumblebee visits on an inflorescence the more nectar it should have obtained from each flower and the more nectar it should have obtained from the inflorescence as a whole.

Bumblebees rarely visit more than four or five flowers on an inflorescence of either of the two plant species studied and, because of this, I have divided the number of flowers visited per inflorescence into four categories, namely, 1, 2, 3, and $\geq 4$ flowers. Each one of these categories would include many of the $x_i$ in the model but, if they are labeled $x_1, x_2, x_3$, and $x_4$ (i.e., $x_i = i$ flowers/inflorescence), then the properties of the optimal movement pattern still apply. Hence the above prediction becomes for bumblebees and inflorescences that the mean angular deviation of the distribution of $\theta$, the difference between the directions of arrival at and departure from an inflorescence, should increase toward an asymptote as the number of flowers visited on the inflorescence increases.

![Fig. 4](image)

**Fig. 4.** The mean angular deviations of the distributions of changes in direction at inflorescences are plotted against the number of flowers visited per inflorescence for movements of workers of *Bombus flavifrons* (a) and queens of *Bombus appositus* (b) between inflorescences of *Aconitum columbianum* and *Delphinium nelsoni*, respectively. The numbers alongside each point are the sample sizes corresponding to each point.

This prediction is also well supported by the available data. In Figs 4a and 4b the mean angular deviations ($S$) of the distributions of $\theta$ are plotted against the number of flowers visited per inflorescence for movements of *Bombus flavifrons* and *Bombus appositus* between inflorescences of *Aconitum columbianum* and *Delphinium nelsoni*, respectively. In both cases $S$ increases as the number of
flowers visited per inflorescence increases and in one case appears to reach an asymptote. The trends in both cases are significant at the 5% level (Spearman rank order correlation test).

(4) The fourth prediction is that the mean distance moved from one resource point to the next should decrease toward an asymptote as the amount of energy obtained at the first resource point increases. Since the mean distance from one resource point to the next is a decreasing function of the sector width employed at the first resource point (Eq. (3)) and the optimal sector width increases toward an asymptote as the amount of energy obtained at the resource point increases (Eq. (17)), the above prediction follows immediately. Using the above estimate of the amount of energy obtained by a bumblebee at an inflorescence this prediction is now, for the present situation of bumblebees and inflorescences, that the mean distance moved by the bumblebees from one inflorescence to the next should decrease toward an asymptote as the number of flowers visited on the first inflorescence increases.

This fourth prediction is also well supported by the available data. In Fig. 5 the mean distance $d$ flown by *Bombus flavifrons* workers between successive inflorescences of *Aconitum columbianum* is plotted against the number of flowers visited on the first inflorescence. It can be seen that $d$ decreases as the number of flowers visited per inflorescence increases and that $d$ appears to reach an asymptote. The trend is significant at the 5% level (Spearman rank order correlation test). Hence all predictions made with the present level of memory are supported by the available data.

*Memory level 4.* Knowledge of the directions of arrival at the present
resource point and at the one immediately before the present one and of the amount of energy obtained at the present resource point.

As the memory of an animal is assumed to increase in capacity, the number of possible memories that can be considered becomes very large. However, a reasonable extension to the previous memory level would seem to be the addition of a knowledge of the direction of arrival at the next to last resource point. So it will now be assumed that an animal has a knowledge of the directions of arrival at both the present resource point and at the one immediately before it and of the amount of energy obtained at the present resource point.

With this addition to the animal’s memory, the frequency $f$ with which resource points are revisited is no longer a function simply of the correlations between the arrival and aimed departure directions and between the aimed and actual departure directions. Instead $f$ will now be a function of the directions of the last two movements, the aimed departure direction and the correlation between the aimed and actual departure directions; i.e.,

$$f = f(\delta_1, \delta_2, \delta_3, h)$$

(19)

where $\delta_1$ is the direction of arrival at the next to last resource point, $\delta_2$ is the direction of arrival at the last resource point, $\delta_3$ is the direction of aimed departure from the last resource point, and $h$ is the correlation between the aimed and actual departure directions.

With the present level of memory and its associated new form for the quantity $f$ the prediction that the sector width should increase with increases in the amount of energy obtained remains intact (i.e., Eq. (17) still holds). For, since $f$ increases with decreases in the tendency of the animal to maintain a straight line course and increases with any increases in the overall tendency to change direction (Pyke, 1976a), then $f$ will increase as $h$ decreases (i.e., the relevant part of Eq. (12) still holds). The derivation of the prediction then proceeds exactly as before.

Any relationship between the above three directions that decreases the overall tendency of the animal to change direction will increase the net rate of energy gain ($E$) and hence would be predicted to occur. As argued above such a relationship would decrease the frequency $f$ of revisitation and hence, by an analysis identical to that employed in the derivation of Eq. (18), would result in an increase in $E$.

The relationship between the three directions that would decrease the overall tendency of the animal to change direction is where the animal tends to alternate left and right turns by adjusting its aimed departure direction. Such alternation of turns could easily be achieved if the animal simply aims its departure from a resource point somewhat clockwise or counterclockwise of the arrival direction if the last change in direction were counterclockwise or clockwise, respectively. This relationship between the directions of aimed departure and arrival would
not result in perfect alternation, however, since the actual departure direction can be quite different from the aimed departure direction. Hence the model predicts that, if the animal had this level of memory, the animal would tend to alternate left and right turns.

This prediction is in fact borne out by the available data. Figures 6a and 6b show the number of times that left- or right-hand turns were followed by left- or right-hand turns for the cases of Bombus appositus and Bombus flavifrons foraging amongst flowers of Delphinium nelsoni and Aconitum columbianum, respectively. In both cases right turns tend to be followed by left turns and vice versa. This tendency is significant at the 5% level in the first case but is not significant at the same level in the second case (Fisher Exact Test). A larger sample size would, possibly, reveal that the tendency in the second case is also significant.

In the case of the previous memory level predictions were derived with respect to the relationship between the amount of energy obtained at a resource point and both the mean angular deviation of the change in direction at a resource point and the mean distance moved from one resource point to the next. Predictions were also derived with respect to the forms of the distributions of the distances between and changes in direction at resource points. With the present enlarged memory and the associated alternation of right and left turns, these predictions are unaltered.

(1) The prediction that the mean distance moved from one resource point to the next should decrease as the amount of energy obtained at the first resource point increases depends solely on the sector widths and not at all on the relationships between the various directions. Hence this prediction is preserved since, as argued above, Eq. (17) still holds.
(2) The prediction that the frequency distribution of distances moved between successive resource points should be similar in shape to that given by the equation \( F(d) = \gamma d \exp(-\gamma d^2/2) \), depends solely on the fact that there is a frequency distribution of sector widths. Hence it holds regardless of any properties of the various directions or of the sector widths.

(3) The frequency distribution of the difference between the directions of arrival and aimed departure should be unimodal, symmetric, and have a mean of \( 0^\circ \) since a clockwise change in direction at a resource would be best compensated for by a counterclockwise change of similar magnitude and vice versa. The distribution of the change in direction at a resource point can then be shown for any sector width to be unimodal and symmetric and to have a mean angle of \( 0^\circ \). Hence the overall distribution of this change in direction should have the same properties. The mean angular deviation of the distribution of changes in direction can also be shown to still be an increasing function of the sector width employed. Hence, since Eq. (17) still holds, it is still predicted that this mean angular deviation should increase with increases in the amount of nectar obtained at a resource point. Thus, as claimed, all these previous predictions remain intact, and, as shown in the previous section, the available data support them well.

Other memory levels. The data presented above indicate that the memory of a bumblebee that is foraging for nectar extends at least to a knowledge of the direction of arrival at the present inflorescence (i.e., resource point), the change in direction at the previous inflorescence and the amount of energy (i.e., nectar) obtained at the present inflorescence. In certain circumstances a bumblebee’s memory is likely to be even greater than this. For example, in some situations an animal visiting resource points may have a “memory” which includes a “knowledge” of the exact location of a number of these resource points. If the density of resource points were sufficiently low that a “naive” animal would spend large amounts of time searching for resource points, then the advantage to the animal, in terms of foraging efficiency, of a “knowledge” of the exact locations of resource points would be great. This “knowledge” would probably be of little advantage if the density of resource points is high because then the search time would be essentially zero. Also, if the number of resource points visited on a foraging bout is large then an animal would probably be unable to “remember” the locations of all the resource points. Thus we would expect to find animals exhibiting a “knowledge” of the exact locations of resource points when (i) the density of resource points is low and (ii) the number of resource points visited per foraging bout is small (perhaps because the food gain per resource point is very high). This appears to be true for euglossine bees visiting tropical plants with low population densities (Janzen, 1971) and for bumblebees visiting plants in low densities (Manning, 1956; personal observations). Also, when the density of flowers or groups of flowers is high, as in the present study,
individual bumblebees will pass through an area many time and visit flowers or
groups of flowers in the area in a very different sequence each time and do not
exhibit a "knowledge" of exact locations of the resource points (Manning, 1956;
personal observations). So this phenomenon does not affect the results of the
present study.

So far, however, no other extensions to the memory have been explored
theoretically, nor have any data been collected that would indicate that bumble-
bees do in fact have a greater memory. These remain problems for the future.

Some additional predictions. The following result is established if \( \partial E/\partial w \), is
differentiated with respect to \( \lambda_1, \lambda_2, (\lambda_1 - \lambda_2) \), and \( \rho \) when \( w_i = \hat{w}_i \):

\[
\frac{\partial}{\partial \lambda_1} \left[ \frac{\partial E}{\partial w_i} \right]_{w_i = \hat{w}_i} = -\frac{\partial}{\partial \lambda_2} \left[ \frac{\partial E}{\partial w_i} \right]_{w_i = \hat{w}_i} = \frac{\partial}{\partial (\lambda_1 - \lambda_2)} \left[ \frac{\partial E}{\partial w_i} \right]_{w_i = \hat{w}_i} > 0; \\
\frac{\partial}{\partial \rho} \left[ \frac{\partial E}{\partial w_i} \right]_{w_i = \hat{w}_i} < 0.
\]

(20)

Hence \( \partial \hat{w}_i / \partial \lambda_1 \) and \( \partial \hat{w}_i / \partial (\lambda_1 - \lambda_2) \) are greater than 0, while \( \partial \hat{w}_i / \partial \lambda_2 \) and
\( \partial \hat{w}_i / \partial \rho \) are less than 0 (for all \( i \)). Thus the optimal sector widths \( \hat{w}_i \) all increase as
the cost of movement between resource points (\( \lambda_1 \)) increases, as the cost while
at the resource points (\( \lambda_2 \)) decreases, as the excess of the cost of movement over
the cost while at a resource point (\( \lambda_1 - \lambda_2 \)) increases, or as the density of resource
points (\( \rho \)) decreases, everything else remaining constant.

If \( S_i \) and \( d_i \) are the mean angular deviations of the frequency distribution
of \( \theta \) and the mean distance between successive resource points, respectively,
which correspond to \( s \), units of energy obtained per resource point (i.e., to \( w \)),
then the following predictions are obtained from the above result: With increases
in \( \lambda_1 \) or \( (\lambda_1 - \lambda_2) \) or with decreases in \( \lambda_2 \), all the \( S_i \) should increase and all the \( d_i \)
should decrease. At the same time the overall mean angular deviation \( S \) of the
distribution of changes in direction at resource points should increase and the
overall mean distance \( d \) between successive resource points should decrease.
With decreases in \( \rho \) all the \( S_i \) and also \( S \) should increase but it is not possible
to say what should happen to the \( d_i \) and to \( d \) because these are functions both of
the \( w_i \) and of \( \rho \).

No data are presently available to test any of these predictions. Such tests are
also problems for the future.

Conclusion

The data presented above indicate that the memory of a foraging bumblebee
extends at least to a knowledge of the direction of arrival at the present inflorescence,
the change in direction at the previous inflorescence (or the direction
of arrival at the previous inflorescence), and the amount of energy obtained at the present inflorescence. The data also support the hypothesis that nectar foraging bumblebees will be found to employ rules of movement which maximize the net rate of energy gain. The predictions that arise from this basic hypothesis for the above level of memory and which have now been tested are listed below:

(i) If $\theta$ is the direction of actual departure minus the direction of arrival, then the distribution of $\theta$ (for all resource points) should be unimodal, symmetric, and have a mean angle of 0°.

(ii) The overall distribution of distances moved between successive resource points should be strongly leptokurtic.

(iii) If $\theta_i$ is the direction of actual departure minus the direction of arrival for a resource point at which $x_i$ units of energy are obtained, then the mean angular deviation ($S_i$) of the distributions of $\theta_i$ should increase toward an asymptote with increasing $x_i$.

(iv) If $d_i$ is the mean distance moved by an animal from one resource point to another when it obtains $x_i$ units of energy at the first resource point, then these $d_i$ should decrease toward an asymptote with increasing $x_i$.

(v) The animal should tend to alternate right and left turns. All these predictions are well supported by the available data.

A couple of alternative explanations might be proposed for the results which agree with the above predictions. None of these, however, adequately explain the results.

(1) While a bumblebee is moving from one flower to another within an inflorescence its memory of its direction of arrival at the inflorescence might decay with time. This hypothesis would predict the observed increases in the mean angular deviation of the change in direction at an inflorescence with increases in the number of flowers visited on the inflorescence. The hypothesis would not, however, predict the observed decreases in the mean distance moved from one inflorescence to the next with increases in the number of flowers visited at the first inflorescence.

(2) Bumblebees might move between inflorescences by simply tending to aim each departure from an inflorescence in a constant compass direction and then employing a scanning sector (of variable width) to choose the next inflorescence. This hypothesis could explain all of the results listed above. This hypothesis could not, however, explain the frequent changes in the general direction of a bumblebee's path. Furthermore, it would predict that the occasional complete reversals of direction by the bumblebees (see Figs. 2a and 2b) should tend to be followed by another compensatory reversal of direction. Such is not the case for the 11 complete reversals of direction (i.e., "S" movements) were
followed by 4 N, 2 NE, 3 NW, 1 E, and 1 W movements and there were no S, SE, or SW movements. Any of these latter movements could reasonably be considered compensatory reversals. Thus after a complete reversal of direction the bumblebees tended to keep going in the new direction rather than resuming the old. The same is true for movements which are almost complete reversals (i.e., SE and SW movements). Hence the bumblebees were not tending to maintain a constant compass direction.

Bumblebees are known to restrict their foraging activities to certain areas to which they may return repeatedly for periods of up to several days (Free and Butler, 1958; Heinrich, 1975; personal observations). These observations do not, however, conflict with the present study because, when bumblebees are foraging in very large patches of plants as in the present study, they are not found to observe definite boundaries but rather they tend to be seen repeatedly in the same general area. Furthermore, this tendency to be seen repeatedly in the same general area is probably a result of a tendency on the part of the bumblebees to always commence their foraging at about the same point for each foraging bout. Hence the overall movements of foraging bumblebees can be predicted on the basis of their tending to commence each foraging bout at a fixed location and then moving according to the rules determined above which maximize their net rate of energy intake.

**Summary**

(1) Natural selection should have favored those bumblebees which, while exclusively collecting nectar, behave in general in ways that maximize their net rate of energy gain (i.e., that are optimal). The aim of the present study was to test the more particular hypothesis that nectar-feeding bumblebees, while moving from one inflorescence to another, will employ the optimal rules of movement and exhibit the optimal pattern of movement.

(2) The optimal pattern of movements is derived from a mathematical model. This model shows that the optimal movement pattern is a function of the level of memory that the bumblebee is assumed to possess. In choosing the next inflorescence a bumblebee might have a knowledge only of its direction of arrival at the present inflorescence (i.e., short memory) or it might have a knowledge of the directions of many previous movements and of the amounts of nectar obtained at many previous inflorescences (i.e., long memory). The model is developed in stages, each successive stage corresponding to a greater level of memory. At each stage the predicted optimal movement pattern is compared both with the predictions for previous memory levels and with available data. These data were collected for workers of *Bombus flavifrons* and queens of *B. appositus* collecting nectar from *Aconitum columbianum* and
Delphinium nelsoni, respectively, and were obtained near the Rocky Mountain Biological Laboratory, Crested Butte, Colorado.

(3) Field data indicate that the memory of a nectar-collecting bumblebee extends at least to a knowledge of the direction of arrival at the present inflorescence, the change in direction at the previous inflorescence, and the amount of energy obtained at the present inflorescence. The data also support the hypothesis that nectar-collecting bumblebees will be found to employ rules of movement which maximize the net rate of energy gain.

ACKNOWLEDGMENTS

I wish to thank S. Altmann, F. Frost, S. Hubbell, D. Janzen, R. Levins, R. Lewontin, M. Price, R. Pulliam, M. Slatkin, O. R. Taylor, and R. Jander for help and criticism during the course of this work. I would also like to thank the Rocky Mountain Biological Laboratory for providing facilities and an excellent scientific atmosphere during my field studies. This research was supported by a grant from the Ford Foundation to the Department of Biology at the University of Chicago and by a grant from the Hinds Fund of The University of Chicago. S. Altmann, E. Charnov, D. Janzen, R. Pulliam, and M. Slatkin have made useful comments on earlier versions of this paper but the faults remain my own.

REFERENCES


