

The foraging ecology of hoverflies (Diptera, Syrphidae): circular movements on composite flowers

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Summary. An energetic analysis of the foraging behaviour for nectar of *Eristalis tenax* L. is presented. The rate of energy gain while foraging on *Aster* is low (0.01 W) relative to similar calculations for bees, but the flies can fill their crop in about 75–220 min. Flies visit the nectar-bearing ring of florets on a capitulum systematically, leaving when they have circled it once (Fig. 1). A simple decision-making rule appears to be used to decide when to leave.

Introduction

It has become customary to look at organisms from the standpoint of energetics (Heinrich 1975a, b), in order to gain insight into behaviours that may or may not appear adapted to the conservation of energy (e.g. Heinrich 1979a, b); the energetic savings made possible by behaving in certain ways and not others can be very large (Heinrich 1981, p. 274). Such an approach is particularly useful for studying nectarivores since their foods are relatively easily characterised in terms of energy.

The natural extension of this view is to develop mathematical models, and to extract solutions using some principle of 'optimisation' (Pyke et al. 1977). However, Gould (1980) believes that "... organisms are not optimising machines; they are historical objects, constrained by inherited Baupläne, modes of development, and mechanical properties of building materials (...). Models based on optimal diets are most interesting when we can explain why organisms do not match them".

Movements between flowers or inflorescences have been the subject of numerous models (Pyke 1978a, b, 1981a, b; Waddington and Holden 1979; Marden and Waddington 1981) which have at-

tempted to predict the directions and distances of movement and the number of flowers probed per inflorescence. In some cases, authors have suggested that foragers move randomly, e.g. non-territorial sunbirds (Gill and Wolf 1977).

Hoverflies favour the capitula of composites in their visits to flowers, and these capitula can be regarded as patches of resources, each made up of many florets. It is interesting therefore to look at the way in which a nectar-feeding individual probes the florets and flies between capitula. The results can be viewed in the light of models of optimal movement. Such a system is particularly convenient because it is two-dimensional; previous studies have perforce confounded the two separate movements in the circular and horizontal directions. Very few studies have measured the movements of hoverflies between flowers, and these have always been in the context of pollination (Minderhoud 1951; Williams and Free 1974). *Eristalis tenax* L. is a suitable species for this study, since most of its visits to flowers are to obtain nectar (Gilbert 1981b).

Materials and methods

The foraging of the drone-fly, *Eristalis tenax* L., on patches of a large-flowered variety of *Aster novae-angliae* was studied in early September 1980, in Cambridge, England. Movements were recorded by observation, noting the time on the capitulum, the number of florets visited, the angle and distance to the next capitulum visited (angles measured relative to the previous direction of flight), and the number of degrees of florets probed on the 360° circle of florets.

Sampling for nectar was accomplished with 1- μ l microcapillaries (CamLab Ltd., Cambridge, England) drawn out so as to be ultra-thin (width ca. 0.2 mm). Samples were taken from florets unprotected from insect visits. The sugar concentration (in sucrose equivalents, gms per 100 gms nectar) was determined with a hand-held refractometer (Bellingham & Stanley, Tunbridge Wells, Kent, England) modified to accept volumes as low as 0.05 μ l. The effects of other refractile substances was

assumed to be negligible (Inouye et al. 1980). Nectar determinations were obtained from *Aster* during a single day. The average amount of nectar present per hour declined during the day, probably as a result of bumblebee foraging; figures given here refer to the average amount over the whole day.

Estimates of energy expenditure during flight were obtained from flight-mill experiments similar to those of Hocking (1953): the flies flew steadily for about 30 min, allowing fairly accurate estimates of weight-loss. Oxygen consumption during flight was also measured, using flies that were tethered but supporting their own weight (see Gilbert 1981a). Oxygen concentrations were determined using a Taylor-Servomex OA272 paramagnetic oxygen analyser.

Results

Nectar availability

The development of disc-florets in composites is described by Proctor and Yeo (1973, p. 220) and can be summarised thus. Disc-florets are arranged on the capitulum in a complex logarithmic spiral (Dixon 1981), but essentially they mature in rings, starting with the outermost. Thus at any one time the capitulum consists of immature unopened florets in the middle, a ring (usually single) of florets producing pollen, then a few rings of florets at the stigmal stage, and on the outside the brown and shrivelled florets that are no longer attractive to insects. Pollen is presented by being pushed out of the anther tube by stylar growth, and is stimulated by insect visits (Proctor and Yeo 1973).

Aster capitula were sampled for nectar by probing the pollen-producing florets. No floret at any other stage contained nectar. Even in the pollen-bearing florets, most contained no fluid at all (223 of 251 probes), even early in the morning (0830 BST). Those that did have nectar (11.2% of florets) had an average of 0.0052 mg sucrose equivalents, about 0.09 J of energy (range, 0.02–0.31 J). These figures are similar to those recorded by Heinrich 1975a, 1976) and K  pyl   (1978) for unprotected flowers: the large amounts that accumulate in flowers protected from insect visits have been documented by Pesti (1976).

Foraging movements

On arriving at a capitulum, *E. tenax* usually ingests a little pollen. It then travels round the flower, systematically probing the florets of the pollen-bearing ring, though it often fails to probe every floret. Depending on the position of the body when landing, the fly may stand at the centre and turn on the spot, or may walk round the edge of the head. Having regained the point at which it started, there is nearly always a change in behaviour: the

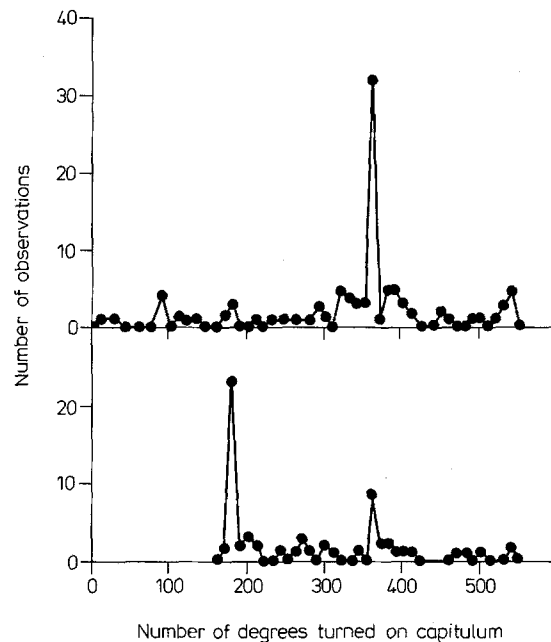


Fig. 1. Female *Eristalis tenax* foraging on a large-flowered variety of *Aster-novae-angliae*. *Upper*: the number of degrees of florets probed on the capitulum, with zero set by the first flower probed. *Lower*: the number of degrees of florets probed after the capitulum has been turned 180° in the direction of circling (see text)

fly leaves the capitulum, stops to groom, or reverses the direction of circling.

The nectariferous ring can be regarded as a circle of 360°, with the zero set by the initial probe. Most individuals leave having completed one set of probings (Fig. 1). Reversals of direction are not included in Fig. 1, and were less than 5% of observations. Flies circled clockwise or anticlockwise, apparently at random.

The energetics of foraging

The rate of energy utilisation during flight on the mill was between 11.9 and 15.3 W N⁻¹. These data can be compared with the measured rates of oxygen consumption, where the three estimates were 55.4, 53.3, and 49.7 ml O₂ hr⁻¹ g⁻¹, equivalent to about 30 W N⁻¹ if the respiratory quotient is unity. Sotavalta and Laulajainen (1961) give a value of 14 W N⁻¹ for *E. tenax*, and their datum was probably used by Weis-Fogh (1973), who quotes 13.4 W N⁻¹. The reliability of these figures has been discussed elsewhere (Gilbert 1981a). The mean mass of *E. tenax* is 125 mg: thus here I shall take 0.02 W as a likely figure for the rate of energy utilisation during flight.

Flight times between capitula averaged 1.43 ± 0.58 s (*n* = 145); an average inter-capitular flight therefore requires about 0.03 J.

These data allow a rough estimate of the energetics of foraging in *E. tenax*. Since only 1 in 9 florets contains 0.09 J, then assuming that florets actually containing nectar are randomly distributed in the nectariferous ring, on average *E. tenax* covers its requirements for flight between capitula by visiting 3 florets per head. The actual number probed per head (Fig. 2) is very variable and is possibly bimodal; the average number is 19, containing on average 0.19 J. *E. tenax* can therefore make a large profit, even at these low nectar availabilities.

The rate of visiting florets on one head was on average $0.92 \pm 0.39 \text{ s}^{-1}$; thus to visit 19 florets and fly to the next head took on average about 20 s. For *E. tenax* foraging on *Aster*, therefore, an energetic profit of approximately 0.01 W was possible. Average and maximal crop volumes were 5.8 and 17.2 μl respectively, with an average concentration of 40% (Gilbert 1981 a). If all the crop contents were derived from continuous foraging on *Aster*, the length of time required to obtain the average and maximal volumes would be about 75 and 220 min respectively.

How do they know when to leave?

It seems paradoxical that *E. tenax* can leave the capitulum so precisely, when nearly all the florets are empty. The marginal value theorem predicts that the fly will leave when the rate of gain of energy drops to the average for the habitat. Hoverflies do not appear to assess the amount of nectar that they obtain from florets for several reasons. Firstly, most florets are empty, and those with nectar contain such small amounts that it is difficult to imagine a physiological basis for the monitoring. Second, if the capitulum (unpicked) is turned slowly by hand against the direction of movement of the fly while the insect is still circling, departure is normally delayed and the same florets may be probed up to 4 times before the fly eventually leaves. Finally, if the head is turned in the direction of circling, the fly normally leaves early, before 360° of florets have been visited.

Counting movements in the direction of circling as positive, 3 conditions can be compared: unmanipulated flowers, flowers turned +90° and then -90°, and flowers turned +180°. The following criteria were used to identify disturbances and exclude them from the data: disturbances by other insects; where the fly stopped to groom for more than 1 s; where the fly was not circling before, during, and after the manipulation; and where the fly reversed its direction of circling.

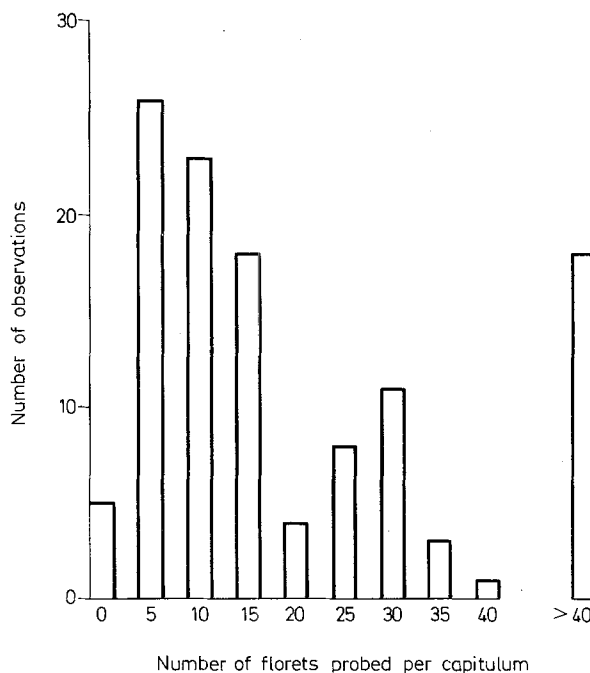


Fig. 2. The number of florets probed per capitulum by female *E. tenax* foraging for nectar on *Aster*. Numbers on the abscissa refer to the upper end of the range, i.e. '10' = 'between 6 and 10 florets probed'.

Few data were collected for the +90°, -90° manipulation, since for some reason the incidence of 'disturbance' was high. In the cases that fulfilled the criteria, all flies left the head after probing about 360° ($n=15$). The results presented here therefore refer to a comparison between unmanipulated flowers and those moved +180°, and are preliminary until a valid set of control data have been obtained. I did not have the impression that flies merely departed away from the observer, and it would be difficult to interpret all the results of this were the case.

The frequency distribution of the number of degrees of florets probed for the +180° manipulation is shown in Fig. 1. The two distributions of Fig. 1 are significantly different (Kolmogorov-Smirnov test, using the unmanipulated case as the 'expected' distribution, $D=0.42$, $n=66$, $P \ll 0.001$). Thus when the flower is turned half-way round, the flies leave when only half the usual number of florets has been probed. These data suggest that, far from monitoring nectar levels, the flies rely on an external reference mark to indicate when the full circle has been visited.

Further evidence that it is unlikely that *E. tenax* monitors nectar levels is the significant proportion of revisits (at least 6% of 405 visits); one individual visited one capitulum 7 times, an-

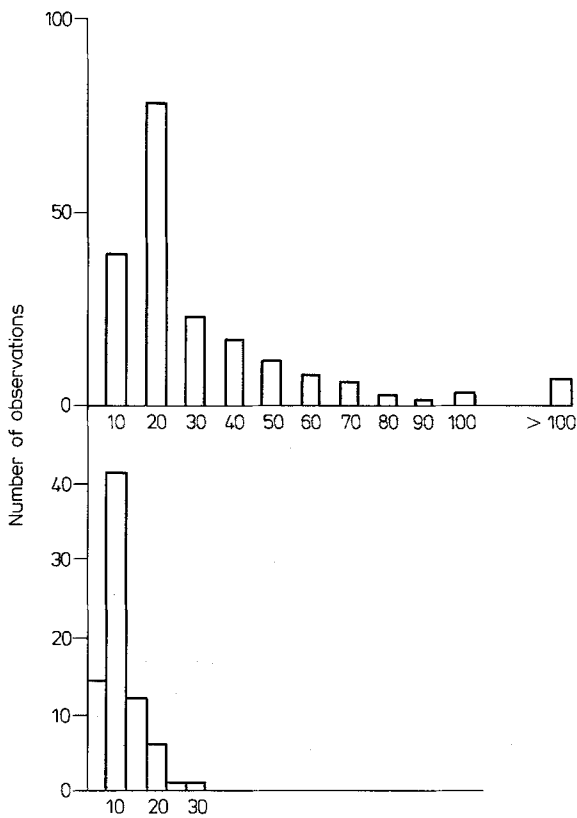


Fig. 3. Upper: the inter-capitular distances flown by female *E. tenax* in the *Aster* patch. Lower: the nearest-neighbour distances between capitula of *Aster* (all cms)

other 5 times, and yet another 4 times during one sequence of 78 visits.

Directionality

Flight distances show a leptokurtic distribution, as do the nearest-neighbour distances between capitula (Fig. 3). *E. tenax* does not merely fly to the nearest head, as can be adduced from a comparison of the two distributions.

No patterns could be discerned in the directions between lines of flight. If the previous departure direction (relative to arrival direction to an *Aster* capitulum) had been to the left, then the subsequent departure direction was to the left 59 times, to the right 53 times, out of 112 instances. If the previous departure direction had been to the right, then the subsequent departure direction was to the left 56 times, to the right 47 times, of 103 instances. These differences are not significant ($G=0.06$). Thus no consistent 'zig-zagging' occurred in the flight paths of foragers. The distribution of leaving directions relative to arrival direction is shown in Fig. 4; right and left sides have been added together since they show no discernable differences. For *E. tenax*, the angle between directions of departure and arrival normally lies in the range 10 to 80°.

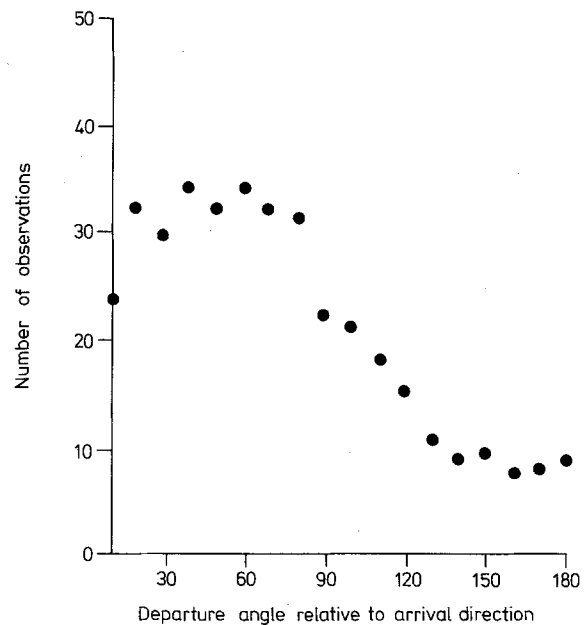


Fig. 4. 'Directionality' in the movements of female *E. tenax* foraging on *Aster*; the data have been smoothed by taking a three-point running average

Discussion

Bees tend to leave inflorescences in the same direction as they arrived, with slight turns alternating right and left during the foraging path (Pyke 1978a). Pyke used these data to support a mathematical model based on the principle that bees forage in such a manner as to maximise their net rate of energy gain. The movements of other foragers have also been interpreted in this way (Pyke 1981a, b; Zimmerman 1981). The usual assumption for such an energy maximisation principle is that animals are able in some way to monitor their food intake (Waddington and Holden 1979). *E. tenax* does not appear to monitor food levels, at least at the level of the individual floret or capitulum. Optimal foraging models also often assume random sampling by animals in order to obtain information about the profitability of patches. Here, *E. tenax* forages systematically in a manner that seems to preclude responses to variation in reward distribution, at least at the level of the floret or capitulum. Instead, it appears to use a simple rule to decide when to leave the capitulum.

The strong directionality exhibited by *E. tenax* may be the result of their manner of systematic searching. Since the flies circle once, and then leave, inevitably they tend to leave more or less in the same direction as they arrived. This may be the optimal strategy too from the point of view of energy maximisation, but it appears not to be a result of assessment by the foragers.

What might be the external cue used by *E. tenax* in its circling of capitula? An obvious candidate is the direction of the sun: circling occurs when the sun is obscured, and therefore the plane of polarisation might be a likely cue. Structural, physiological, and behavioural evidence indicates that flies are able to distinguish the plane of polarisation, and this has been confirmed in *E. tenax* (Horridge et al. 1975).

The candidature of the polarisation plane should be regarded as a working hypothesis. Wellington (1976) interpreted the behaviour of territorial male *E. tenax* as a response to the changing pattern of polarisation in the sky during the day. Physical landmarks, however, remain a possibility; *E. tenax* is known to have a sophisticated spatial memory (Collett and Land 1975).

The rate of energy gain obtainable by *E. tenax* foraging on *Aster* (0.01 W) can be compared with the calculations of Heinrich (1975a, Table 2) for bumblebees. He found that the possible energetic profit ranged from about 1.4 W on *Vaccinium* to about 0.01 W on *Kalmia*, and noted that bumblebees only occasionally visit flowers where their average rate of gain is less than 0.02 W. Solitary bees were the main visitors to these low rewarding flowers; hoverflies appear to be similar in their tolerance of low rates of energy gain.

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