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Flower visiting by hoverflies (Syrphidae)

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Abstract

An account is given of a study of resource-partitioning in hoverflies (Syrphidae) which feed almost exclusively on flowers. Suggestions are made for school project work using hoverflies.

1. Introduction

Grinnell (1914) probably first stated the principle that no two species may coexist if they have exactly the same requirements of their environment, that is, the same ecological niche. This has come to be known as the principle of competitive exclusion. Gause (1934) studied the population dynamics of two species of *Paramecium* which compete with one another when in mixed culture, resulting in the suppression of one of the two species, and he wrote:

> '. . . as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor . . .'.

The principle of competitive exclusion has a great value in drawing to our attention the ways in which a community divides the resources of the habitat between its constituent species; implicit in the studies reviewed by Schoener (1974) is the opinion that the observed pattern of partitioning is the result of competitive interactions, such as one species depleting another's resources, interfering with its ability to obtain those resources, or using up in aggressive encounters energy obtained from them. This assumption is by no means always true. As Schoener pointed out, niche separation can result from other mechanisms too; for example, natural selection for reproductive isolation, or divergence for avoiding 'habit-forming' predators. However, several studies have shown that competition can maintain differences of habitat, for example, in barnacles (Connell, 1961).

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The concept of the ecological niche can be used to investigate the hoverflies (Fam. Syrphidae), which feed almost exclusively from flowers, using their tongues to reach into the corollae of the blooms for nectar, or eating pollen either directly from the anthers or by combing it from the long body hairs to which the pollen adheres. There are about 250 species of hoverflies in Britain, active from early spring to late autumn; the few species investigated have been found to be important pollinators, for instance, in *Plantago*, the plantains (Stelleman and Meeuse, 1976). There is scope for school projects, either early or very late in the school year, on the pollinating abilities of the different species and on more general ecological questions. The use of keys and the challenge of taxonomy can be taught with Coe's (1953) handbook.[1]

2. Method

This study of resource partitioning in the hoverflies started in September 1977 with observations on a patch of wasteland in Clacton-on-Sea, Essex, on flowers of fennel (*Foeniculum vulgare*), ragwort (*Senecio jacobaea*), knapweed (*Centaurea nigra*), goldenrod (*Solidago canadensis*), and Michaelmas daisies (*Aster cf. novae-angliae*). The hoverfly species were chosen for convenience of identification at a distance, and some of the 'species' may have included several closely related species: these are indicated by 'cf.'. The species were:

(a) wasp mimics
- *Syrphus cf. vitripennis*
- *Metasyrphus cf. corollae*
- *Episyrphus balteatus*
- *Helophilus pendulus*
- *Sphaerophoria cf. scripta*

[1] Although the keys by Coe (1953) are straightforward for the identification of most of the common species of hoverflies, there are some difficult areas. Fortunately a new and comprehensively illustrated manual is being prepared by Alan Stubbs of the Nature Conservancy Council for publication in 1981, and the book will contain keys that are much easier to use.

(b) honey-bee mimics *Eristalis tenax*
Eristalis arbustorum
Eristalis nemorum

The flowers chosen were in patches of approximately equal area. These were observed at random half-hour periods between 10.00 h and 15.00 h on seven days between 8/9/77 and 14/9/77. In retrospect it might have been better to start observations at dawn, at about 05.00 h. The number of visits, as defined by landings on the patch, was recorded for 10–30 mins, all results being tabulated 'per half-hour'. The sexes of *Sphaerophoria*, easily distinguished in the field, were recorded separately.

Hoverfly specimens were preserved in alcohol and their tongue lengths measured. The corolla depths of the flowers (the distance from the lip of the corolla to the lowest point to which a very long-tongued fly could reach) were obtained from the literature (Knuth, 1906–9; Müller, 1883).

The object in collecting the data in this way was to answer three questions:

(a) Do different species of hoverflies visit different flowers?
(b) Are the different species active at different times of the day?
(c) Is tongue length connected with the choice of flower?

The data were arranged in five tables, each table giving the number of visits to a flower type for each of the nine species (with a tenth row for 'others') subdivided between the ten time periods.

3. Results and discussion

(a) Flowers visited

The average number of visits per half-hour of each fly species to each flower was calculated, and converted to percentages (*Table 1*). The visiting patterns fell into three main categories according to the flowers that attracted the greatest number of visits:

(a) mainly *Foeniculum* and *Solidago*, rather less to *Senecio;*
(b) mainly *Solidago* and *Senecio*, rather less to *Centaurea;*
(c) mainly *Senecio* and *Aster*.

Groups (a) and (c) correspond to the generic groups *Syrphus* (*S. vitripennis*, *M. corollae*, and *Ep. balteatus*) and *Eristalis* respectively, and group (b) to *Sphaerophoria* and *Helophilus*. The two commonest species, *Episyrphus balteatus* and *Eristalis tenax*, are particularly well separated in this manner: the hypothesis that their distribution on the flowers is due to chance is tested by 'chi-squared' on the original numbers, giving a value of 417.3 for 4 degrees of freedom, and a value greater than 18.5 arises by chance with a probability of less than 0.001. The 'others' consisted mainly of *Scaeva pyrastri*, *Melanostoma scalare*, *Platycheirus*, and *Syritta pipiens*, and constituted an insignificant proportion of the total number of visits.

(b) Separation in time

Having found partitioning of the available flowers between the genera, we can again look at the concept of the niche. This suggests that individuals of the most closely related species compete to a greater extent than those of less closely related species. The overall number of visits recorded in each time period is given in percentages in *Table 2*. Ideally, the number of visits in each time period results from the addition of values from each flower species. Unfortunately it was not possible to record in all time periods from each flower, and the deficiencies are indicated in the row labelled '*n*', the number of times records were obtained from any particular time period. The

Table 1. The percentage of visits to the flowers by each hoverfly species

Species	*Foeniculum*	*Solidago*	*Senecio*	*Aster*	*Centaurea*
S. vitripennis	38	37.5	10	14.5	0
Ep. balteatus	28	22	28.5	1.5	20.5
M. corollae	36	43	19	2	0
E. tenax	0	3.5	35	29	32.5
E. arbustorum	2	15	49.5	33.5	0
E. nemorum	0	0	6	94	0
H. pendulus	0	22	39	6	32
Sph. scripta (f)	8	35	28	3	26
Sph. scripta (m)	3.5	55.5	36	0	5
'Others'	15.5	32	45	8	0

Table 2. The percentage of visits during each time period by the hoverfly species

Species	½-hour time periods from 10.00 h 1	2	3	4	5	6	7	8	9	10
S. vitripennis	0	0	6	6	0	13.5	26	27	9	12
Ep. balteatus	6	17.5	14.5	14	12	4	5.5	9	14	4
M. corollae	0	15.5	4	3	13.5	13	9.5	8.5	20	13
E. tenax	7	9	11.5	12	7	6.5	8	12	14	14
E. arbustorum	6.5	10.5	11	9	10	6	10.5	11.5	12	14
E. nemorum	7	7	16	7	8	8	13	8	13	13
H. pendulus	6	7.5	6.5	4	11	6	9	7.5	21.5	21
Sph. scripta (f)	14	9	10	17	25	3	3	0	11	8
Sph. scripta (m)	9	3.5	5.5	15.5	25.5	5	7.5	6	12.5	10
'Others'	4.5	14.5	11.5	10	20	6	7	5	11	10
n	3	3	3	4	3	1	5	4	2	7

lack of data was remedied in an *ad hoc* fashion by filling in the gaps using data from the adjacent periods, such that each figure used in calculating the percentages in *Table 2* was made up from the sum of single records from each flower. For example, if no record was obtained for the period 11.30 to 12.00 h for *Solidago*, then the number of visits recorded in the period 11.00 to 11.30 h was used as an estimate for the missing value.

As can be seen from *Table 2*, the *Syrphus* species (*S. vitripennis*, *M. corollae*, and *Ep. balteatus*), badly separated from each other by flower type (*Table 1*), separate very well between the time periods. For the *Eristalis* species, *E. nemorum* stands apart from the other two by virtue of visiting *Aster* almost to the exclusion of the other four flowers, whereas *E. tenax* and *E. arbustorum* are more general in the pattern of their visits. The degree of separation between these last two appears to be small, but calculation of the 'niche overlap' according to the method of Pianka (1973) indicates that the degree of overlap between them in just these two dimensions of time and flower type is adequate to permit coexistence (accepting the argument of May and MacArthur, 1972) without considering other flowers in the area or other dimensions to their niches. Stelleman and Meeuse (1976) found that the optimal period for the flower visits of *Melanostoma* and *Platycheirus* was in the early hours of the morning after sunrise: it may be that the two *Eristalis* species would have been better separated had these times been included in the study.

(c) Tongue length

The final question concerned the role of size, as measured by the length of the tongue, in the separation of the species. Hutchinson (1959) found that the ratio of the sizes of the trophic apparatus of several orders of animals was no smaller than 1.28, and proposed that this represented the limiting similarity between species. The tongue lengths of the species in this study are shown in *Table 3*, and the corolla depths of the flowers in *Table 4*. A weighted average for each fly species was calculated by multiplying each percentage in *Table 1* by the depth of the corolla of the relevant flower and summing for each fly

Table 3. Tongue lengths of the species in the study

Species	Tongue length (mm)	S.D.	*n*
S. vitripennis	2.26	0.11	7
Ep. balteatus	1.80	0.08	10
M. corollae	2.28	0.05	3
E. tenax	5.06	0.14	11
E. arbustorum	3.51	0.07	5
E. nemorum	2.67	0.18	4
H. pendulus	2.73	0.14	2
Sph. scripta (f)	2.31	0.08	7
Sph. scripta (m)	2.47	0.44	6

Table 4. Depths of the corollae of the flowers (from literature)

Species	Depth (mm)
Foeniculum	0
Solidago	1.5
Senecio	2.75
Aster	3.0
Centaurea	4.0

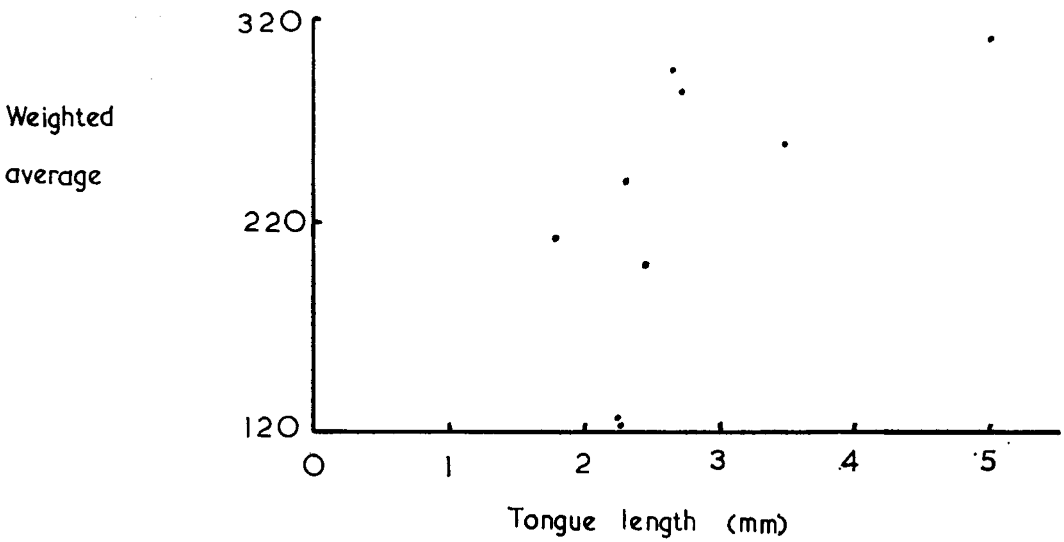

Fig. 1. The relationship between the tongue length of the eight species of hoverfly and the corolla depths of the flowers they visit. The corolla depths are weighted according to the percentage of visits paid to them by each species (for details, see text).

species. This average is plotted against the length of the tongue in *Fig. 1.*

An ordinary product-moment coefficient of correlation for this regression is not significant, probably due to the fact that there are only nine points in the regression. However, Kendall's coefficient of rank correlation shows that it has a probability of less than 2.2 per cent of arising by chance alone (one-tailed test). Part of the mechanism of flower choice could therefore be that flies tend to choose flowers whose nectar they can easily exploit. Recent work has shown that the nectaries are very rapidly depleted in the morning by foraging insects, mainly bees, and that for the rest of the day only small quantities of nectar are secreted (Heinrich, 1975; Corbet, 1978a and 1978b), hence the importance of being able to reach to the bottom of the corolla.

Sphaerophoria males appear to have a much more variable tongue length than the females, which may allow them to exploit different resources from them and thus avoid competing. The males were twice as frequent visitors to the flowers of the study, but any differences were of degree only.

4. Conclusions and suggestions for further work

Hoverflies share the resources available to them partly by visiting different flowers on the basis of matching their tongue lengths with the depth of corollae of the flowers that they choose, and partly by being active at different times of the day. However, this leaves open the more fundamental question of how these differences are determined. The insects could be responding to any or all of three variables: an inherent rhythm of activity and 'preference'; the weather; or some attributes of the flowers, possibly the rewards. These could be affected by climate, an inherent secretory rhythm affecting the characteristics of the nectar, or an inherent rhythm affecting the presentation of pollen. Recently it has been shown that it is not adequate to add together the results from different days, because the rewards of the flowers change during the day and from day to day (Corbet, 1978a and 1978b; Corbet, Unwin, and Prŷs-Jones, 1979); it is thus necessary to record in cycles of whole days, and to keep these cycles separate. The present study suffers from this defect, and yet the short period over which it was conducted consisted of sufficiently similar conditions for the results to have yielded some interesting conclusions.

It is suggested therefore, that a valuable sixth-form project could be to investigate the factors affecting the differences in the visiting of flowers. Simple but effective techniques exist to measure some of the variables involved. Modified refractometers for the measurement of the sugar concentration of nectars are available from the firm of Bellingham and Stanley Ltd, Tunbridge Wells, Kent TN2 3EY; two ranges are needed, 0–50 per cent, and 40–85 per cent. Microcapillaries will measure the volume of nectar present, and can be bought from Camlab Ltd, Nuffield Road, Cambridge CB4 1TH; the one-microlitre size will be needed. Equipment for small-scale recording of variations in temperature and relative humidity has been designed by Dennis Unwin, the details of which have been published (Unwin, 1978; Corbet, Unwin, and Prys-Jones, 1979).

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