

## On the abundance of hoverflies (Syrphidae)

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Hoverfly populations are more stable than those of published analyses of other invertebrate groups. The data show clearly the importance of removing the dependence of the variance on the mean before analysis.

The abundance and stability of different larval feeding types (predators, phytophages, saprophages), and of generalists and specialists are discussed. The abundance and stability of the feeding types are not different. Specialization of habitat leads to lower abundance, but has no detectable consequences upon stability. Among predators, extreme specialists are least abundant and generalists are most abundant; both have less stable populations than moderate specialists.

There are strong correlations between abundance and distribution, and between local and regional distributions. Abundance is not affected by body size, but larger species tend to have more stable populations.

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### Introduction

In the last 25 years community ecology has attempted to describe theoretically the patterns that exist in Nature. Most community theory considers populations at equilibrium only (Connell and Sousa 1983), yet universally insect populations are known to fluctuate from week to week, and year to year. Many of the concepts and theories of community ecology have nevertheless been applied to insects, and indeed were first inspired by insects (Hutchinson 1959).

Are animal populations really at equilibrium? This argument over stability has recently resurfaced with some tests in the work of Connell and Sousa (1983) and Wolda (1983). In the view of these authors, stability means a relative constancy of numbers with time, rather than mere persistence (i.e., not dying out completely). Connell and Sousa (1983) conclude that arthropod populations are not less stable than bird or mammal populations. Schoener (1985, 1986) and Ostfeld (1988) disagree on the basis of their data from lizards, spiders and mammals, showing that the distribution of stability in the vertebrate groups is significantly shifted towards

greater stability than in terrestrial arthropod populations. Wolda (1983) compared the fluctuations in abundance of tropical insects with temperate ones, and found no differences.

How stable therefore are insect populations? Long-term data are invaluable for answering this and other questions about populations that are highly relevant to generating realistic ecological theory. Some of these questions have recently been addressed in the literature. Redfearn and Pimm (1988), for example, ask whether the degree of polyphagy affects the variability of insect population sizes; other authors ask about the relationship between distribution and abundance (Hengeveld and Haecck 1982, Brown 1984, Schoener 1987).

This study analyses population fluctuations of one family of flies (hoverflies, Diptera: Syrphidae) sampled intensively over fifteen years in an English suburban garden. We address the following questions:

- 1) how stable in size are hoverfly populations on an annual basis? How does this compare with other groups that have been studied?

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- 2) does larval feeding type, habitat or degree of specialization influence population size or its variability?
- 3) what is the relationship between geographical distribution and population size/stability?
- 4) is larval life-style related to distribution?

The family is particularly suited to answering some of the above questions because of its wide variety of larval feeding habits coupled with relatively uniform adult feeding habits (see Gilbert 1986).

## Methods

The main data come from weekly Malaise-trap samples collected between 1 April and 31 October over the last 15 yr by J. O. from a suburban garden: details of the garden and trapping protocol have been published elsewhere (Owen 1981, 1983, Owen and Owen 1975), where there is a full discussion of the nature of the catch. We use two different data sets here for analysis. The first is the full data set of 91 recorded species over 15 yr of weekly catches (780 wk, assuming no catches for winter weeks); the second is the subset of 40 commoner species caught more than 30 times in total over the 15 yr. To these data are added morphological, and adult and larval feeding data. Morphological data on size and shape are available for the 33 commonest species, derived from a previous study (Gilbert 1985a) which gives details of the variables concerned. Adult feeding was characterized for each species as pollen or nectar specialization, or mixed feeding, from Gilbert (1981, 1985b) or from unpublished data. Larval habitat was scored for all species, and feeding specialization for predators. Habitats were scored as leaf-litter, herbs, trees, herbs or trees, enclosed (subterranean or galls), Lepidopteran aggregations, tree-holes, aquatic or semi-aquatic decay situations, plants or social-insect nests (see Gilbert 1986): the feeding specializations of predatory species were scored by Dr. G. E. Rotheray (Royal Museum of Scotland, Edinburgh) on the basis of his extensive field experience, as highly specialized, moderately specialized, or generalized (where adequate data exist to make a firm decision).

Differences in abundance or in abundance fluctuations between species grouped in these categories were tested with one-way analysis of variance using the statistical package BMDP (Dixon 1983). We used annual totals, were log-transformed in all cases. Where an F-test is invalid because group variances were not equal (using Levene's test), we use Welch's test for assessing the equality of means (see Dixon 1983).

We used both Connell and Sousa's (1983) and Wolda's (1983) methods for assessing the stability of populations from year to year; both involve analysing the variability of log-transformed data. Connell and Sousa (1983) used the standard deviation of log-transformed census data as their index of stability of numbers; Wolda (1983) used the mean of the logarithms of the variance

of the log-transformed abundances, his 'stability index'. Our standardized data avoid the problem recently highlighted by Pimm and Redfearn (1988), namely that estimates of variability increase with the number of years included in the data set.

We checked first to see if particular weeks or years were aberrant, by using TWINSPAN, a Cornell Ecology Program (Hill 1979) for two-way indicator species analysis. This produces a classification of species and samples in a tabular matrix that approximates a Braun-Blanquet phytosociological table. In this way the  $15 \times 52 = 780$  wk of data were classified according to their similarity in hoverfly catch, and then species were classified according to how diagnostic they are for each division of the classification of weekly samples. Species can only be handled on a 'presence/absence' basis, and so the standard way of including relative abundances is to create 'pseudospecies' (see Hill 1979, Jongman and ter Braak 1987) of different levels of abundance. In the run reported here, levels of 0, 10, 50, 100 and 200 were used; on this basis a species recorded less than ten times during any one week will be represented by one 'pseudospecies', whereas as species recorded more than 200 times in any one week will be represented by five 'pseudospecies'.

Distributional data for the U.K. are in a rudimentary form at present, although provisional maps are being prepared by the Hoverfly Recording Scheme at the Biological Records Centre, Monks Wood. The only available quantitative data on hoverfly distributions come from surrounding countries: Belgium (Verlinden and DeClerf 1987), the Netherlands (Barendregt 1982), Schleswig-Holstein (Claussen 1980), Denmark (Torp 1984), and Ireland (Speight 1983). Overall distributions were obtained by simply summing together all records for the number of squares (usually 10 km<sup>2</sup>, and adding 100 when a species was also recorded from Siberia (from Violovitsh 1983) to try to incorporate an element for species with wide Palaearctic distributions).

## Results

### Patterns of abundance fluctuation

TWINSpan produces a two-way table of species and samples. The table here is 91 species  $\times$  780 wk, an impractical size for reproduction. Its salient features only will be noted. The main division is between the early weeks of most seasons (weeks 16–19) and the rest; these early weeks are characterized by *Platycheirus ambiguus*, joined in some years by other species such as *P. scutatus*, *P. albimanus*, and *Pipiza noctiluca*. Most weeks and species are classified in the 'rest', which is further subdivided. The first of the two divisions contains weeks 30–41 with the characteristically high abundance of late summer; diagnostic species are *Episyrphus balteatus*, *Metasyrphus corollae*, *Eristalis* spp., *Eumerus* spp., and *Platycheirus albimanus*. The other grouping

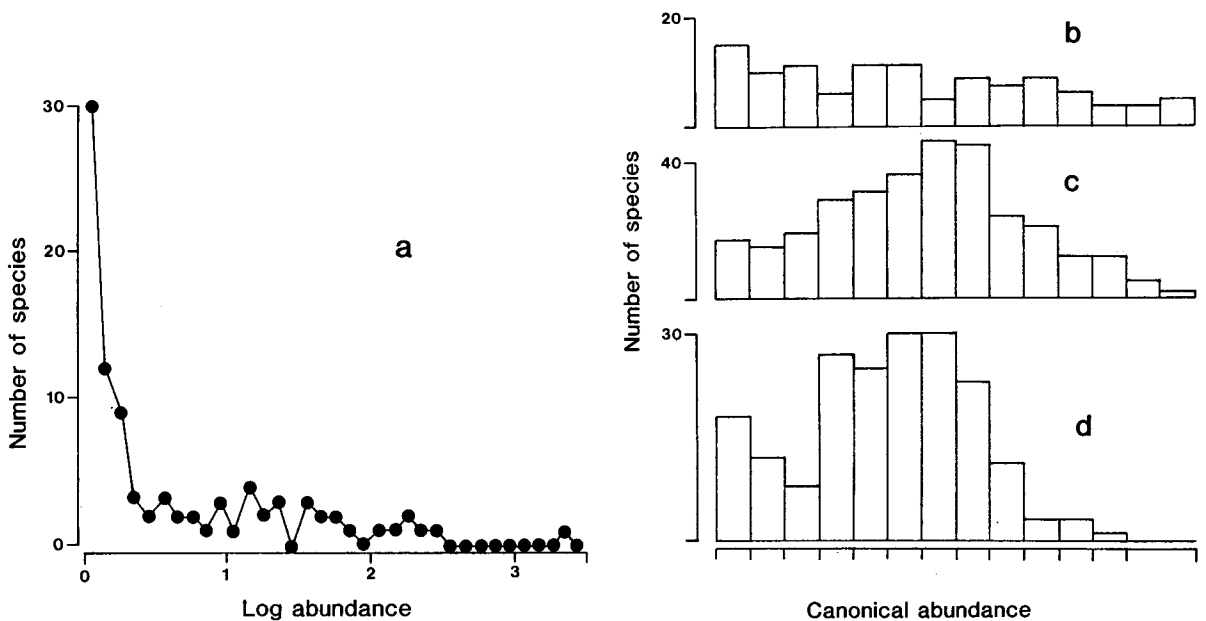


Fig. 1. Frequency distribution of log-abundance for hoverfly data from Leicester (all 91 species), Belgium and Schleswig. (a) Frequency distribution from Leicester, ordinate on a log-scale; (b), (c) and (d) frequency distributions of data from 15-yr study at Leicester, Belgium and Schleswig, respectively, ordinate on a canonical scale, with categories of abundance of 1, 2, 3-4, 5-8, 9-16, 17-32, etc.

contains weeks on either side of the late-summer peak; first, early summer (characterized by species such as *Merodon equestris* and *Dasysyrphus albostriatus*, and low abundance of *Metasyrphus corollae* and *Syrirta piplens*); and second, autumn stragglers such as *Eristalis tenax*, *E. pertinax*, and *Helophilus pendulus*. The results of this analysis are encouraging in that no one year or groups of years were singled out as being completely different from any others. We are therefore justified in treating years as replicate time-series.

#### General patterns

As expected, there were many rare species but few common ones, conforming to the pattern seen from similar data in other studies (Fig. 1 (a)). Fig. 1 (b, c, d) show the same distribution in canonical form together with distributions of data from Belgium and Schleswig (largely museum compilations). There are clear differences between the compilations of data (c, d) and this standard-sampling programme (b) in that the latter has a very flat distribution. Thus, there are many fewer species with intermediate levels of abundance than expected.

Again as expected, species accumulate with sampling time (Fig. 2), analogous to a rarefaction curve. An obvious conclusion is that one year's sampling gives little idea of the true nature of the garden community.

To find out whether species that were common in one year were also common in the subsequent year, the abundances of species within years were ranked, and

Kendall's coefficient of concordance was calculated for the rankings of the 15 yr. There was a highly significant value for this coefficient ( $W = 1.44$ ,  $\chi^2_{39} = 406.8$ ,  $P \ll 0.001$ ) indicating that overall the rank abundances are preserved from year to year.

#### Stability of syrphid populations

The time-series for each of the 40 commoner species were examined for trends by regressing annual abundance against time; with such multiple tests, we set the

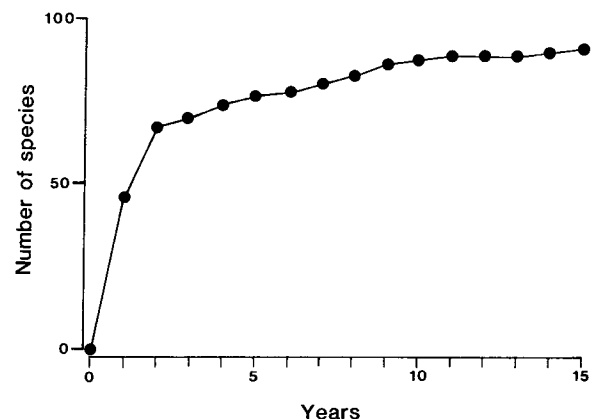


Fig. 2. Discovery of new species of hoverfly over the 15 yr of sampling in Leicester.

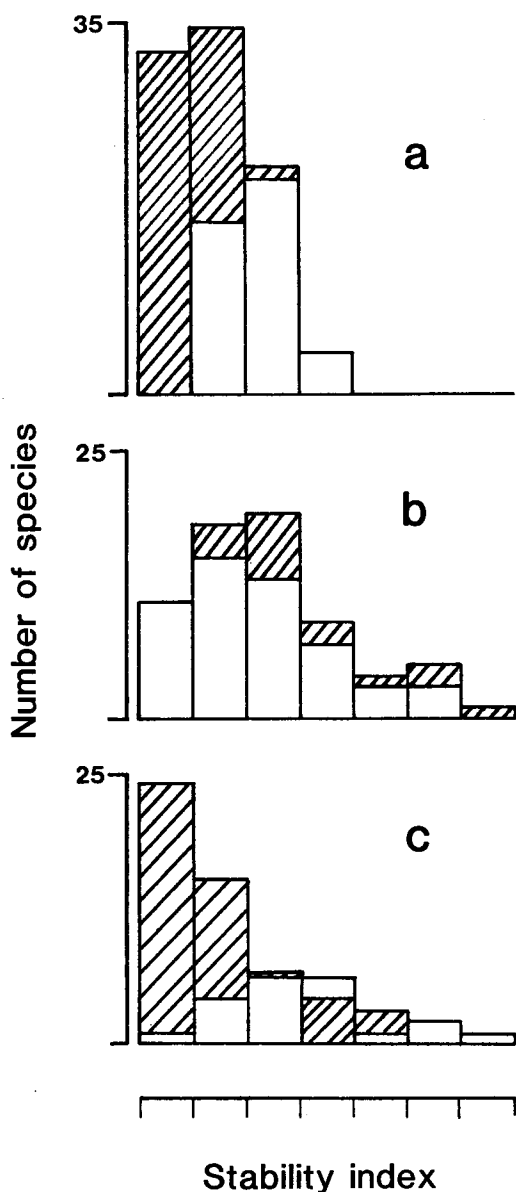


Fig. 3. Distribution of the stability index of Connell and Sousa (1983) for hoverfly species at Leicester. The stability index is the standard deviation of  $\log_{10}$  (census numbers + 1); low values indicate stable populations. Categories of stability are in multiples of 0.2. Hatched and open columns start from zero. (a) Data from syrphids in Leicester, all 91 species (hatched bars) or only the 40 species recorded more than 30 times (open bars). (b) Data from Connell and Sousa (1983) for annuals (hatched bars) and annuals except insects (open bars). (c) Data from Ostfeld (1988) for terrestrial vertebrates (hatched bars) and terrestrial arthropods (open bars).

significance level at  $P = 0.01$  to try to avoid mistaking random coincidences for correlation. With this level, only one species, *Platycheirus ambiguus*, had a significant slope ( $b = -5.48 \pm 1.32$ ,  $P < 0.001$ ), indicating that its numbers were declining throughout the study period.

As Taylor (1961) and many others including Wolda

found (Fig. 2 in Wolda 1983), there is a strong relationship between the untransformed variance and the mean annual abundance, plotted on a log-log plot (for the 40 common species: slope =  $1.90 \pm 0.07$ , intercept =  $0.215 \pm 0.108$ ,  $F_{1,38} = 727$ ,  $P \leq 0.001$ ); this accounts for almost 95% of the scatter. When the data for the 40 commonest species are log-transformed, there is no relationship between the variance and the mean ( $F_{1,38} = 1.94$ , n.s.), also as Wolda found (cf. Fig. 3B in Wolda 1983). However, the variance of the data for all 91 species is not stabilized by a log-transformation, since there remains a strong variance - mean relationship ( $F_{1,89} = 106.9$ ,  $P \leq 0.001$ ) which accounts for 54% of the scatter: this is an important point, as will become apparent later.

Fig. 3 (a) gives the distribution of the standard deviations of log-census numbers, and this figure can be compared with Connell and Sousa's data (Fig. 3b). Fig. 3 (a) gives the distributions for all species and just the 40 commoner species: the two distributions are significantly different (Kolmogorov-Smirnov test,  $D = 0.36$ ,  $P < 0.01$ ), demonstrating that the subset of 40 species have higher variances in abundance. Wolda (1983) notes that rare species cannot help but have low variances for purely statistical reasons, and Connell and Sousa (1983) point out that their index is sensitive to low values (although they made no attempt to allow for it). This means that great care is needed before conclusions can be drawn about differences in stability between different groups, if some species are rare.

In all comparisons with Connell and Sousa's (1983) data (with all species, with just annuals, and with non-insect annuals: Fig. 3b), the distribution for the full 91 species is very significantly different ( $D > 0.23$ ,  $P \leq 0.01$ ), with syrphids being more stable. This we assume to be an artefact of including all species, however rare. The distribution of variances of the commoner 40 syrphid species does not differ from Connell and Sousa's whole set ( $D = 0.18$ , n.s.), nor from just annuals ( $D = 0.19$ , n.s.), but does possibly differ from the set of non-insect annuals ( $D = 0.2125$ ,  $P = 0.06$ ) in that there are fewer low variances than expected. Again the arbitrary nature of excluding 'rarer' species means that little significance can be attached to this difference (see Discussion).

The compilation of data in Ostfeld (1988) was also used for comparison with the temporal variability of syrphid populations. Ostfeld's compilation (Fig. 3c) is divided into vertebrates and arthropods; the distribution of the index of variability for the 40 commoner species of syrphid is significantly different from the former ( $D = 0.46$ ,  $P < 0.001$ : more high values) and from the latter ( $D = 0.38$ ,  $P < 0.05$ : fewer high values). However, the distribution of variability for all 91 syrphid species is not significantly different from Ostfeld's terrestrial vertebrates ( $D = 0.11$ , n.s.), and has significantly fewer high values than his terrestrial arthropods ( $D = 0.49$ ,  $P < 0.01$ ). Thus, depending upon whether one includes or excludes rare species, syrphid populations can be made to seem just as stable as those of

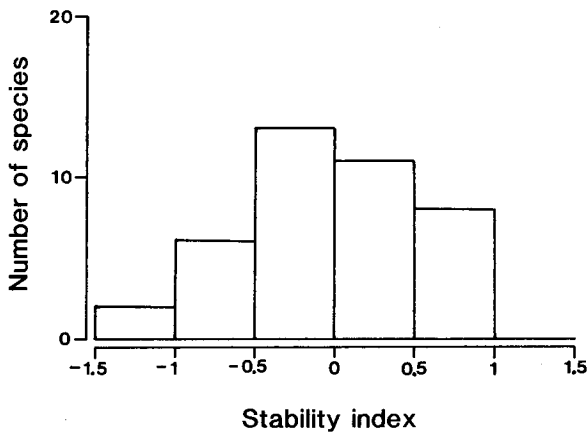


Fig. 4. Frequency distribution of values of Wolda's (1983) stability index (see text) for hoverflies trapped in the garden at Leicester.

vertebrates; they are certainly more stable the arthropod populations noted by Ostfeld (1988).

Wolda's (1983) stability index was calculated for the same data (Fig. 4). For the commoner 40 species, there is no difference between the stability index of Wolda's temperate insects (see Fig. 5B in Wolda 1983) and syrphids ( $D = 0.13$ , n.s.). We conclude that our data are representative of temperate insect populations.

#### Abundance patterns and ecological groupings

We looked for relationships between both abundance and variability in abundance, and features of the size and life-history of the various species. We predicted that large (Peters 1983, Morse et al. 1988) or more specialized species (in habitat or in food type: Brown 1984) would have lower abundance. We also predicted that certain categories of larval habitat type or degree of feeding specialization should have more stable populations than others. In particular, tree-hole species and generalists should have more stable populations: tree rot-holes are a classic example of a rare but highly stable habitat, being used year after year by the same species of syrphid (e.g. holes in Scots pine by *Callicera rufa*: Rotheray, pers. comm.). Generalists should be able to buffer their populations by prey switching (MacArthur 1955). In keeping with the predictions of r- and K-selection (see Gaston and Lawton 1988), we hypothesized that large species should have more stable populations.

#### Patterns of abundance

If larval food habits are divided into three categories (predators, saprophages, and phytophages), there are no significant differences in abundance between these groups ( $F_{2,37} = 0.20$  n.s.: Fig. 5). No differences were found in the abundance of species with different adult foods (Welch  $F_{2,18} = 0.23$ , n.s.). There are highly significant differences between the different guilds of larval

habitat (Welch  $F_{8,24} = 30.14$ ,  $P \ll 0.001$ ). As Fig. 5 shows, species that feed in the leaf litter (and which probably feed generally on arthropods rather than being restricted to aphids), or are found in many types of aphid colonies without much habitat preference (Fig. 5, open circles, no. 2), have higher average abundances than species restricted to herb, arboreal or gall/subterranean aphids. Syrphids whose larvae live in tree rot-holes or in social-insect nests are less abundant than those living in situations of general decay, reflecting what is generally true of syrphid communities (e.g. Bánkowska 1980).

Focussing on just the predators reveals that specialized species are the least abundant, moderately-specialized species have intermediate levels of abundance, and polyphagous species have high abundance (Welch  $F_{2,7} = 30.3$ ,  $P \ll 0.001$ ).

There is no correlation between size (head width) and mean abundance ( $r = -0.07$ ,  $n = 33$ , n.s.).

Thus, anything that entails specialization, either in habitat type or predator specificity, leads to low relative abundance, upholding our prediction. The prediction about large species having lower levels of abundance is not supported.

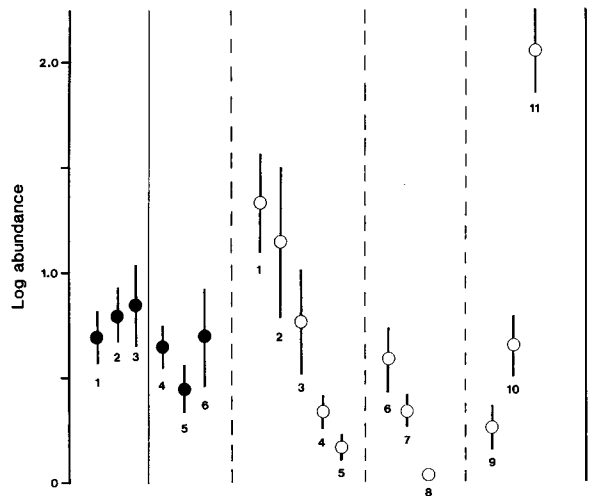


Fig. 5. Average annual log-abundances (with standard errors plotted) for hoverflies trapped over 15 yr in the garden at Leicester. The data are divided into the various guilds.

Solid circles:

1-3 = adult feeding guilds (1 = pollen, 2 = mixed, 3 = nectar),

4-6 = gross larval feeding guilds (4 = predators, 5 = saprophages, 6 = phytophages).

Open circles:

1-5 = predator habitats (1 = leaf-litter, 2 = without much apparent habitat preference, 3 = arboreal, 4 = herb-layer, 5 = in galls or underground),

6-8 = detritivore habitats (6 = general aquatic or semi-aquatic decay, 7 = inquilines in social insect nests, 8 = tree-holes),

9-11 = predator specialization (9 = highly specialized, 10 = moderately specialized, 11 = generalized).

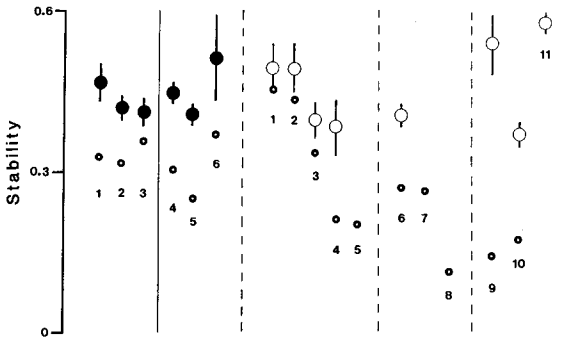


Fig. 6. Average stability (with standard errors plotted) for hoverflies trapped over 15 yr in the garden at Leicester. Divisions as in Fig. 5. Open circles without numbers refer to the appropriate group using data from all 91 species; circles with numbers refer to data from the 40 commoner species (note that certain categories are missing, cf. Fig. 5).

#### Patterns of stability

Very similar patterns are found between groups in variance in abundance. Care is needed, however, because of the problem of the inevitably low variances of rare species. We therefore analyse both the full set of 91 species, and the restricted set of 40 commoner species (where the mean and variance are uncorrelated, but some guilds cannot be assessed due to a lack of data: see Fig. 6).

When all 91 species are analysed (see Fig. 6), adult feeding guilds do not differ in stability (Welch  $F_{2,19} = 0.54$ , n.s.), whereas larval habitat guilds (Welch  $F_{8,18} = 8.36$ ,  $P \leq 0.001$ ) and the degree of predator specialization (Welch  $F_{2,15} = 49.6$ ,  $P \leq 0.001$ ) do differ significantly in stability. When only the 40 commoner species are analysed, larval habitat guilds no longer differ in stability (Fig. 6: Welch  $F_{6,17} = 1.14$ , n.s., several classes with no data), but the degree of predator specialization remains a significant factor (Welch  $F_{2,3} = 20.7$ ,  $P = 0.02$ ). If we take the pattern obtained where we are sure there are no variance-mean problems (40 spp.) as indicating a more reliable picture, then the least variable populations are those whose larvae are moderately specialized; specialized and generalized species have equally high variability in population size.

There is a weak negative relationship between size and variability; thus, larger species tend to have less variable populations ( $r = -0.37$ ,  $P < 0.05$ ), but the proportion of the variance explained is low ( $r^2 = 0.16$ ).

Thus, contrary to the situation with the level of abundance, there are few differences in stability between the various groups. We are unable to assess whether tree-hole species are more stable since they are rare, but our prediction that generalist predators should have more stable populations is falsified. Generalists and narrow specialists have less stable populations than moderate specialists.

#### Abundance and distribution

##### *Are locally widespread species also widespread nationally?*

Using the data provided in Speight (1983) for Co. Laois in Eire, we regressed local distribution (in terms of the number of 10 km<sup>2</sup> squares occupied in Laois) against nationwide distribution (the number of 10 km<sup>2</sup> squares occupied in the whole of Ireland). There is a strong positive relationship between the two variables ( $F_{1,101} = 96.4$ ,  $P \leq 0.001$ : see Fig. 7).

##### *Is a locally abundant species also abundant elsewhere?*

The abundances of species from Leicester are very highly correlated with those from Belgium ( $r = 0.54$ ,  $n = 91$ ,  $P < 0.001$ ) and Schleswig ( $r = 0.50$ ,  $P < 0.001$ ); the slopes of the regression lines (with Leicester abundance as independent variable) are identical (slope = 0.35, log-log regression).

##### *Is a species widespread in one region also widespread elsewhere?*

The recorded numbers of 10 km<sup>2</sup> squares are also highly intercorrelated: using the Belgian records as a reference variable and only using the 91 species recorded from Leicester, there are very high correlations with Schleswig ( $r = 0.78$ ,  $P \leq 0.001$ ), Danish ( $r = 0.88$ ,  $P \leq 0.001$ ) and Irish records ( $r = 0.78$ ,  $n = 65$ ,  $P < 0.001$ ).

##### *Is a locally abundant species also widespread on a large scale?*

Abundances in Leicester are highly correlated with distributional records in Belgium ( $r = 0.54$ ,  $n = 91$ ,  $P < 0.001$ ), Denmark ( $r = 0.54$ ,  $n = 91$ ,  $P < 0.001$ ), Schleswig ( $r = 0.51$ ,  $n = 91$ ,  $P < 0.001$ ) and Eire ( $r = 0.53$ ,  $N = 65$ ,  $P < 0.001$ ).

##### *Does life-style influence distribution?*

Following other authors (e.g. Brown 1984), we predict that specialization of any sort will restrict distribution.

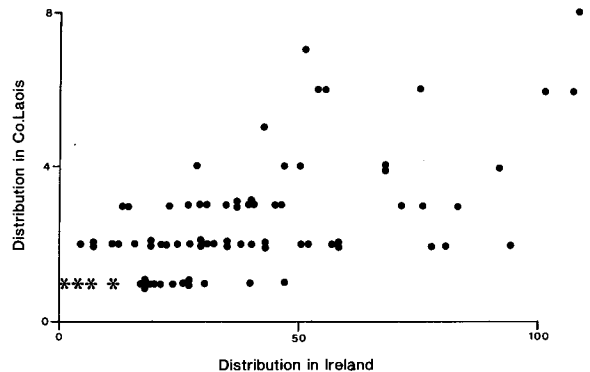


Fig. 7. Relationship between the local distribution of syrphids in Co. Laois (Eire) compared to the overall regional distribution in Ireland. Correlation ( $r = 0.70$ ,  $n = 103$ ,  $P < 0.001$ ). The regression is  $Y = 0.403X + 0.9465$ .

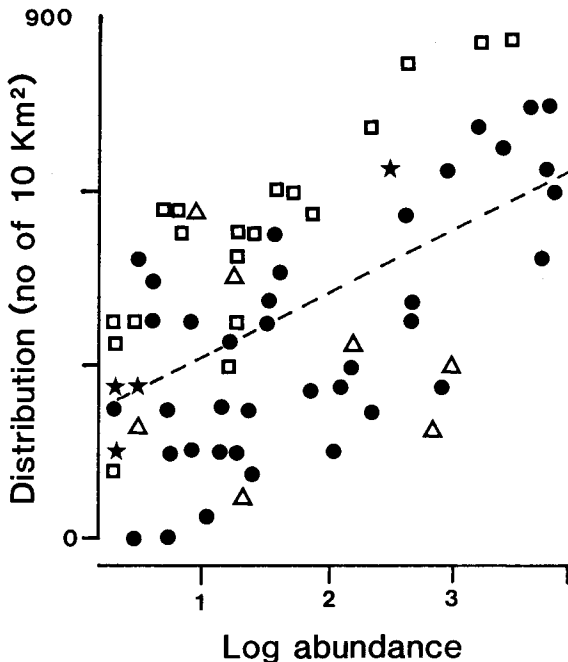


Fig. 8. Relationship between average annual log-abundance of hoverflies in the garden at Leicester and overall distribution. Overall distribution is the summed distribution of Belgian, Schleswig, Danish, Irish and a nominal Siberian distribution. The regression line is shown for all points, but is different for each group (ANCOVA,  $F_{2,72} = 13.0$ ,  $P \leq 0.001$ ). The regression coefficient and intercept are, respectively: - Overall; 116.7, 193; predators; 125.2, 120; saprophages; 193.1, 242; phytophages, regression not significant. Circles = predators, squares = saprophages, triangles = phytophages, stars = multiple points.

Separating species into gross larval feeding categories (predators, saprophages, and phytophages) shows that for all distribution data sets there is a very significant difference in the number of recorded squares overall ( $F_{2,62} = 5.27$ ,  $P < 0.01$ ) and for each dataset separately ( $F_{2,37} > 10.31$ ,  $P < 0.0004$ ), with saprophages always having the widest distribution (e.g. in Belgium, saprophages occur on average in  $237 \pm 53$  squares [34% of all squares], predators in  $141 \pm 74$  squares, and phytophages in  $70 \pm 43$  squares). The regression of overall distribution against abundance in Leicester is different for the three categories (ANCOVA,  $F_{2,72} = 13.0$ ,  $P \leq 0.001$ ; Fig. 8).

There are highly significant differences in distributions between the various larval habitat categories in all regions ( $F > 7.25$ ,  $P < 0.001$ ) and overall ( $F_{8,56} = 7.62$ ,  $P \leq 0.001$ ): species living in many different habitats (predators or saprophages) have the widest distributions (Fig. 9).

Within the predators there is a clear pattern for polyphagous species to have the widest distributions, followed by moderately specialized species, with specialized predators having the most restricted distributions (Welch  $F_{2,6} = 20.36$ ,  $P < 0.01$ ; Fig. 9).

Size is uncorrelated with any set of distributional records, and is also uncorrelated with total distribution.

## Discussion

The results reported here are relevant to the debate about the stability of animal populations. Connell and Sousa (1983), Wolda (1983) and Schoener (1985) make the point that their measure of stability, the standard deviation of log census-numbers, is sensitive to low values; only Wolda (1983) takes this further and excludes species of low abundance whose stability index cannot but be small for mathematical reasons. The effect of this on conclusions about stability is clearly shown in our data. If no species are excluded, the conclusion is that syrphid populations are more stable than those of other terrestrial arthropods, and just as stable as terrestrial vertebrate populations. Once the dependence of the variance on the mean is corrected by excluding rare species, syrphid populations are less stable than Ostfeld's (1988) terrestrial vertebrates, but still more stable than his compilation of terrestrial arthropods. Syrphids are neither more nor less stable than Wolda's (1983) temperate insects. We therefore suspect that (1) Schoener's (1985) and Ostfeld's (1988) conclusions may require modification after particularly rare species have been excluded; and (2) Wolda's (1983) very extensive data set gives a better indication of insect population stability than that of Connell and Sousa (1983). Our data indicate that syrphid populations are no less stable than other insect populations, which are themselves more stable than is implied by the 'terrestrial arthropods' of Ostfeld (1988). It will be interesting to see how these data are integrated with other types of analyses on insect populations; for example, den Boer (1985) suggested that carabid populations were inherently unstable, in many cases only lasting for about ten years.

Not enough is known about the ranges of syrphids to be able to discuss stability in terms of central or marginal species (Hengeveld and Haeck 1982, Williams 1988), but we believe that range limits are not likely to depend upon competition (Gilbert and Owen 1989), but rather

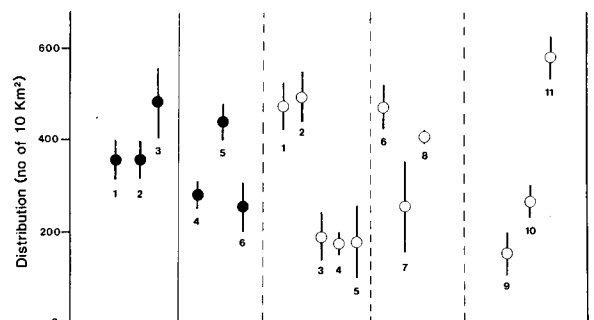


Fig. 9. The average overall distribution of hoverflies of various ecological categories. Overall distribution is the sum of recorded squares from Belgium, Schleswig, Denmark, Ireland, and a nominal addition for Siberia. Categories as in Fig. 5.

on the relationship of physiology with the environment (James et al. 1982, Root 1988).

Lawton (1983) and Strong et al. (1984) discuss the data on rank abundances changing through time: generally rare species remain rare, and common ones remain common. In our data too, rank abundances remain more or less intact from year to year. It is here that perhaps we see indications of a type of 'community structure'. Further analyses may uncover a type of community structure as seen by Simola (1984) in plankton diatoms, where long-term data has uncovered a shifting balance of community structure according to environmental conditions.

The relationship between abundance and distribution is also a topic under active research (e.g. Brown 1984, Williams 1988). Hengeveld and Haeck (1981, 1982) found support for an optimum response-surface model, where the abundance of a species is distributed in an approximately Gaussian manner, centred upon the area where its species-specific abiotic requirements are optimal; i.e. the Grinnellian niche: (James et al. 1984). To this picture they add a further discovery, also found by Rabinowitz (1981), that there is a relationship between abundance and distribution: more abundant species are distributed more widely (see Gaston and Lawton 1988). More widespread species are also less stable (Spitzer and Lepš 1988, Gaston and Lawton 1988).

These findings are further supported by the syrphid data: abundance and stability at the site in Leicester are highly correlated with distribution in western Europe. There are, of course, species that are exceptions, and which point out differences in the sampling strategies employed in the studies whose distributional data are used here. The papers reporting syrphid distributions are compilations of records from many years, mostly from museums. The bias in collecting by dipterists is nowhere more evident than in the grossly inflated number of records for *Cheilosia albitarsis*; while this is a common hoverfly, it is not nearly as common as its museum abundance would suggest. This latter is likely to be caused by collectors paying particular attention to any *Cheilosia* seen because of the chance that it is rare species. Similarly, there is bias in the data from Leicester; for example, the very low abundance of *Myathropa florea* is an artefact of the low efficiency of Malaise traps for catching this species.

Amongst Irish syrphids at least there is a positive relationship between local site occupation and regional distribution (cf. Hanski 1982), and this is related to local abundance. The proportion of the variance accounted for by these relationships is not particularly high (ca. 25%), leaving room for the different types of rare species that Rabinowitz (1981) describes. *Epistrophe grossulariae* is an example of one of her types, i.e. a very widespread species that is a rare component of communities wherever it is recorded. The population dynamics of these widespread rarities is an interesting problem for future research.

Although a negative relationship between local abundance and body size has often been reported (Peters 1983), this was not found by Gaston and Lawton (1988) or Morse et al. (1988) when considering related insect species of one taxon, and is not apparent in the syrphid data; however, mammals do show this relationship (Peters 1983). This points to a possible conclusion that for insect data sets only cross-taxal comparisons appear to produce this relationship. Gaston (1988) thought that a failure to show a relationship between abundance and size was because of the limited range of body sizes in his data: this cannot be the case in the syrphid data, which spans a 400-fold range of weights.

The a priori prediction (Gaston and Lawton 1988) that populations of small species will be less stable is supported by our data, but the relationship is weak, explaining very little of the variance in the data.

What sort of species, therefore, have high abundances, markedly unstable populations, or are widely distributed? What are the consequences of different life-styles on ranges, and population sizes and fluctuations? Few authors have addressed these questions using long-term population data since the pioneering work of Watt (1964) and Rejmanek and Spitzer (1982). Spitzer and Lepš (1988) used the potential growth rate to differentiate between species, finding that this was associated with stability. Redfearn and Pimm (1988) found that the degree of polyphagy of herbivorous insects was either uncorrelated or slightly negatively correlated with population stability.

Data from the Syrphidae are particularly suitable for answering such questions because of the great range of larval feeding habits, but relative uniformity of adult feeding habits. The results are clear:

- 1) *major feeding categories*: the average abundances of the three major feeding types are not different, but saprophages are more widely distributed than predators, which in turn are more widely distributed than phytophages.
- 2) *larval habitat types*: when larval food habits are broken down more finely, certain feeding types have low population sizes and higher stability, although it is difficult to be certain statistically in the latter case since sample sizes are low if the rarer species are excluded to correct variance-mean problems: if they are included the problem influences the patterns obtained.
- 3) *degree of feeding specialization*: Redfearn and Pimm (1988) found no or a slight negative correlation between stability and the degree of polyphagy in Lepidoptera, in complete contrast to Rejmanek and Spitzer (1982) and Watt (1964). In the syrphid data, polyphagous species such as *Syrphus ribesii* have more abundant, less stable populations and are more widely distributed than moderately specialized species such as *Platycheirus scutatus*. The stability of populations of highly specialized predators such as *Platycheirus ambiguus* appears to be just as low as in polyphagous species; only moderate specialization reaps the reward of a more stable population.



Therefore, there seems to be little support for MacArthur's (1955) view that polyphagous species should be buffered against variation in their food supply. A possible explanation for the relative stability of moderately specialized species is that on the one hand specialists are tied to the variability of their hosts, whereas on the other polyphagous species take advantage of host outbreaks (Watt 1964).

Redfearn and Pimm (1988) take great care to avoid categorising a species as specialized merely because it is rare, and therefore host records are few. We believe we too have circumvented this problem by the manner in which the categories were scored, basically through the experience of Dr. G. E. Rotheray; species were scored as 'uncertain' if there was any question about its degree of specialization.

The analysis of long-term population data has great potential for illuminating new facets of adaptation in different species. One aspect of long-term data is the generation of data on distributions; it is now timely to incorporate a spatial dimension to animal ecological theory, but this will be difficult. However, several patterns are becoming clear, such as the fragmentation of populations at the edges of their ranges (Williams 1988). These patterns can only be discovered by obtaining long-term data, the funding for which is well-nigh impossible to obtain. We regard it as essential for future developments in our understanding of the ecology of species and communities that such funding is found and maintained.

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## References

Bánkowska R. 1980. Fly communities in natural and anthropogenic habitats of Poland. – *Memorabilia Zool.* 33: 3–93.  
 Barendregt, A. 1982. *Zweefvliegtabel*. 7e druk. – Uitgave, Jeugdbondsuitgeverij.  
 Brown, J. H. 1984. On the relationship between abundance and distribution of species. – *Am. Nat.* 124: 255–279.  
 Claussen, C. 1980. [The hoverfly fauna of the Schleswig district of Schleswig-Holstein]. – *Faun. Okol. Mitt. Suppl.* 1, 3–79 (In German).  
 Connell, J. H. and Sousa, W. P. 1983. On the evidence needed to judge ecological stability or persistence. – *Am. Nat.* 121: 789–824.  
 den Boer, P. J. 1985. Fluctuations of density and survival of carabid populations. – *Oecologia (Berl.)* 67: 322–330.  
 Dixon, W. J. (ed.) 1983. *BMDM Statistical Software*. – Univ. of California Press, Los Angeles, CA.  
 Gaston, K. J. 1988. Patterns in the local and regional dynamics of moth populations. – *Oikos* 53: 48–57.  
 – and Lawton, J. H. 1988. Patterns in the distribution and abundance of insect populations. – *Nature, Lond.* 331: 709–712.  
 Gilbert, F. S. 1981. Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and

pollen in some common urban species. – *Ecol. Ent.* 6: 245–262.  
 – 1985a. Morphometric patterns in hoverflies (Diptera, Syrphidae). – *Proc. Roy. Soc. Lond. B* 224: 79–90.  
 – 1985b. Ecomorphological relationships in hoverflies (Diptera, Syrphidae). – *Proc. Roy. Soc. Lond. B* 224: 91–105.  
 – 1986. *Hoverflies*. – Cambridge Naturalists Handbooks 5. Cambridge Univ. Press.  
 – and Owen, J. 1989. Population dynamics and ecomorphological relationships in hoverflies. – Submitted to *J. Anim. Ecol.*  
 Hanski, I. 1982. Dynamics of regional distribution: the core and satellite hypothesis. – *Oikos* 38: 210–221.  
 Hengeveld, R. and Haeck, J. 1981. The distribution of abundance. II. Models and implications. – *Proc. Kon. Ned. Akad. Wet. C* 84: 257–284.  
 – and Haeck, J. 1982. The distribution of abundance. I. Measurements. – *J. Biogeogr.* 9: 303–316.  
 Hill, M. O. 1979. *Twinspan* – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. – Cornell Ecology Programs CEP-41, Section of Ecology & Systematics, Cornell Univ., Ithaca, NY.  
 Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many species? – *Am. Nat.* 93: 145–159.  
 James, F. C., Johnston, R. F., Wamer, N. O., Niemi, G. J. and Boecklen, W. J. 1984. The Grinnellian niche of the Wood Thrush. – *Am. Nat.* 124: 17–30.  
 Jongman, R. H. and ter Braak, C. J. 1987. Data analysis in landscape and community ecology. – Pudoc, Wageningen.  
 Lawton, J. H. 1983. Herbivore community organisation: general models and specific tests with phytophagous insects. – In: Price, P. W. et al. (eds), *A new ecology: novel approaches to interactive systems*. Wiley, New York, pp. 206–227.  
 MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. – *Ecology* 36: 533–536.  
 Morse, D. R., Stork, N. E. and Lawton, J. H. 1988. Species number, species abundance and body length relationship of arboreal beetles in Bornean lowland rain forest. – *Ecol. Ent.* 13: 25–37.  
 Ostfeld, R. S. 1988. Fluctuations and constancy in populations of small rodents. – *Am. Nat.* 131: 445–452.  
 Owen, J. 1981. Trophic variety and abundance of hoverflies (Diptera, Syrphidae) in an English suburban garden. – *Holarct. Ecol.* 4: 221–228.  
 – 1983. *Garden life*. – Chatto & Windus.  
 – and Owen, D. F. 1975. Suburban gardens: England's most important nature reserves. – *Environ. Conserv.* 2: 53–59.  
 Peters, R. H. 1983. The ecological implications of body size. – Cambridge Studies in Ecology, Cambridge Univ. Press.  
 Pimm, S. L. and Redfearn, A. 1988. The variability of population densities. – *Nature, Lond.* 334: 613–614.  
 Rabinowitz, D. 1981. Seven forms of rarity. – In: Synge, H. (ed.), *The biological aspects of rare plant conservation*. Wiley, New York, pp. 205–217.  
 Redfearn, A. and Pimm, S. L. 1988. Population variability and polyphagy in herbivorous insect communities. – *Ecol. Monogr.* 58: 39–55.  
 Rejmanek, M. and Spitzer, K. 1982. Bionomic strategies and long-term fluctuations in abundance of Noctuidae (Lepidoptera). – *Acta ent. boh.* 79: 81–96.  
 Root, T. 1988. Energy constraints on avian distributions and abundances. – *Ecology* 69: 330–339.  
 Schoener, T. W. 1985. Are lizard population sizes unusually constant through time? – *Am. Nat.* 126: 633–641.  
 – 1986. Patterns in terrestrial vertebrate versus arthropod communities: do systematic differences in regularity exist? – In: Diamond, J. M. and Case, T. J. (eds), *Community ecology*. Harper & Row, London, pp. 556–586.

- 1987. The geographical distribution of rarity. - *Oecologia* (Berl.) 74: 161-173.
- Simola, H. 1984. Population dynamics of plankton diatoms in a 69-year sequence of annually laminated sediment. - *Oikos* 43: 30-40.
- Speight, M. C. D. 1983. Flies: Diptera. - In: Feehan, J. (ed.), *Laos: an environmental history*. Ballykilcavan Press, Co. Laois, pp. 172-178; 502-507.
- Spitzer, K. and Lepš, J. 1988. Determinants of temporal variation in moth abundance. - *Oikos* 53: 31-36.
- Strong, D. R., Connor, E. F., Simberloff, D. S. and Thistle, A. 1984 (eds) *Ecological communities: conceptual issues and the evidence*. - Princeton Univ. Press, Princeton, NY.
- Taylor, L. R. 1961. Aggregation, variance and the mean. - *Nature*, Lond. 189: 732-735.
- Torp, E. 1984. [The Danish hoverflies (Diptera, Syrphidae)]. Danmarks Dyreliv, Bind 1. Fauna Bøger, København (in Danish).
- Verlinden, L. and DeClerck, K. 1987. The hoverflies (Diptera, Syrphidae) of Belgium and their faunistics: frequency, distribution, phenology. - *Documents de Travail* no. 39. Institut royal des sciences naturelles de Belgique.
- Violovitsch, N. A. 1983. [Siberian syrphids (Diptera, Syrphidae)] *Izdatel'stvo Nauka Sibirskoe Otdeleniye, Novosibirsk* (in Russian).
- Watt, K. E. F. 1964. Comments on long-term fluctuations of animal populations and measures of community stability. - *Can. ent.* 96: 1434-1442.
- Williams, P. H. 1988. Habitat use by bumblebees (*Bombus* spp.). - *Ecol. Ent.* 13: 223-237.
- Wolda, H. 1983. 'Long-term' stability of tropical insect populations. - *Res. Pop. Ecol.* (suppl.) 3: 112-126.

Tab. 1. Classification of hoverfly species trapped in a Leicester garden, incorporating data on abundance, stability, and the categories of larval habitat, predator specialization, and adult feeding guilds.

Species	Annual log <sub>10</sub> abundance		Larval habitat	Predator special.	Adult food
	Mean	SD			
<i>Melanostoma mellinum</i>	2.10	0.63	1	u	1
<i>M. scalare</i>	1.57	0.57	1	u	1
<i>Baccha obscuripennis</i>	0.95	0.28	2	2	1
<i>Platycheirus albimanus</i>	2.44	0.33	1	u	2
<i>P. ambiguus</i>	1.57	0.60	1	1	(1)
<i>P. angustatus</i>	1.33	0.38	1	u	(1)
<i>P. clypeatus</i>	1.85	0.62	1	u	1
<i>P. immarginatus</i>	0.12	0.26	1	u	1
<i>P. manicatus</i>	1.29	0.41	1	2	3
<i>P. peltatus</i>	1.27	0.41	1	2	2
<i>P. scambus</i>	0.13	0.29	1	u	u
<i>P. scutatus</i>	2.33	0.33	2	2	2
<i>Pyrophaena granditarsa</i>	0.27	0.40	1	u	1
<i>P. rosarum</i>	0.02	0.08	1	u	1
<i>Sphaerophoria menthastris</i>	0.46	0.45	2	2	2
<i>S. rueppelli</i>	0.22	0.30	2	u	2
<i>S. scripta</i>	1.77	0.48	2	2	2
<i>Paragus tibialis</i>	0.77	0.48	2	u	(2)
<i>Heringia heringii</i>	0.27	0.26	5	1	u
<i>Neocnemodon vitripennis</i>	0.66	0.48	5	1	(1)
<i>Pipiza austriaca</i>	0.17	0.26	2	(2)	1
<i>P. bimaculata</i>	0.04	0.11	(5)	u	u
<i>P. fenestrata</i>	0.04	0.11	(5)	u	u
<i>P. luteitarsis</i>	0.08	0.14	5	1	u
<i>P. noctiluca</i>	0.81	0.34	2	2	u
<i>Pipizella varipes</i>	0.18	0.28	5	1	u
<i>Triglyphus primus</i>	0.02	0.08	5	1	u
<i>Chrysotoxum bicinctum</i>	0.13	0.17	5	1	1
<i>C. festivum</i>	0.31	0.28	5	1	1
<i>C. verralli</i>	0.29	0.32	5	1	1
<i>Dasysyrphus albostrigatus</i>	0.94	0.22	3	2	2
<i>D. lunulatus</i>	0.08	0.14	3	u	2
<i>D. tricinctus</i>	0.02	0.08	3	(2)	2
<i>D. venustus</i>	0.06	0.12	3	u	2
<i>Epistrophe eligans</i>	1.11	0.31	3	2	1
<i>E. grossulariae</i>	0.02	0.08	3	(1)	1
<i>E. nitidicollis</i>	0.18	0.25	3	(2)	1
<i>Episyrphus balteatus</i>	2.28	0.62	4	3	1
<i>Leucozona lucorum</i>	0.31	0.36	4	2	2
<i>Melangyna cincta</i>	0.29	0.22	3	1	u
<i>M. lasiophthalma</i>	0.11	0.21	3	2	u
<i>M. triangulifera</i>	0.08	0.14	3	2	u
<i>M. umbellatarum</i>	0.03	0.12	2	1	u

cont'd

Tab. 1. Continued

Species	Annual log <sub>10</sub> abundance		Larval habitat	Predator special.	Adult food
	Mean	SD			
<i>Meliscaeva auricollis</i>	0.61	0.49	3	u	1
<i>M. cinctella</i>	0.06	0.12	3	2	1
<i>Metasyrphus corollae</i>	2.23	0.57	4	3	2
<i>M. latifasciatus</i>	0.71	0.50	3	u	u
<i>M. latilunulatus</i>	0.13	0.24	3	u	u
<i>M. luniger</i>	1.59	0.38	(4)	2	2
<i>Parasyrphus punctulatus</i>	0.04	0.11	3	2	(2)
<i>P. malinellus</i>	0.02	0.08	(3)	u	u
<i>Scaeva pyrastris</i>	0.38	0.36	4	2	1
<i>S. selenitica</i>	0.05	0.14	4	2	1
<i>Syrpus ribesii</i>	1.67	0.55	4	3	1
<i>S. torvus</i>	0.04	0.11	3	2	1
<i>S. vitripennis</i>	1.10	0.49	(4)	2	1
<i>Xanthogramma pedissequum</i>	0.02	0.08	5	2	u
<i>Eristalinus sepulchralis</i>	0.10	0.18	8		u
<i>Eristalis abusivus</i>	0.03	0.12	8		u
<i>E. arbustorum</i>	1.79	0.49	8		2
<i>E. horticola</i>	0.25	0.35	8		2
<i>E. intricarius</i>	0.47	0.28	8		2
<i>E. nemorum</i>	0.51	0.41	8		2
<i>E. pertinax</i>	1.00	0.39	8		3
<i>E. tenax</i>	1.18	0.36	8		3
<i>Helophilus hybridus</i>	0.18	0.27	8		2
<i>H. pendulus</i>	1.32	0.40	8		2
<i>H. trivittatus</i>	0.02	0.08	8		2
<i>Myathropa florea</i>	0.07	0.19	7		2
<i>Cheilosia albitarsis</i>	0.13	0.17	9		(1)
<i>C. bergenstammi</i>	0.15	0.35	9		u
<i>C. paganus</i>	0.27	0.26	9		2
<i>C. proxima</i>	0.04	0.11	9		u
<i>C. vernalis</i>	0.53	0.63	9		u
<i>Ferdinandea cuprea</i>	0.04	0.11	(7)		1
<i>F. ruficornis</i>	0.02	0.08	(7)		1
<i>Rhingia campestris</i>	1.08	0.48	8		3
<i>Chrysogaster hirtella</i>	0.02	0.08	8		2
<i>Liogaster metallina</i>	0.24	0.26	8		u
<i>Orthoneura splendens</i>	0.08	0.15	8		u
<i>Neoascia podagrica</i>	0.55	0.43	8		2
<i>Eumerus strigatus</i>	1.35	0.56	9		u
<i>E. tuberculatus</i>	1.50	0.59	9		u
<i>Merodon equestris</i>	1.60	0.26	9		2
<i>Volucella bombylans</i>	0.26	0.24	10		3
<i>V. pellucens</i>	0.28	0.29	10		3
<i>Criorhina floccosa</i>	0.02	0.08	7		u
<i>C. berberina</i>	0.02	0.08	7		u
<i>Syrpitta pipiens</i>	2.05	0.42	8		2
<i>Tropidia scita</i>	0.02	0.08	8		u
<i>Xylota segnis</i>	0.07	0.15	8		1

Key to categories of Tab. 1.

Larval habitat:

1 = leaf litter      2 = herb layer      3 = trees      4 = trees and herbs      5 = confined places  
with aphids  
6 = Lepidoptera col-      7 = tree-holes      8 = aquatic/semi-      9 = living plants      10 = social-insect nests  
onies      aquatic

Predator specialization:

u = not known      1 = highly specialized      2 = moderately  
specialized      3 = generalized

Adults food:

1 = pollen      2 = mixed nectar/  
pollen      3 = mainly nectar      u = not known