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SIZE, SHAPE, COMPETITION, AND COMMUNITY STRUCTURE IN HOVERFLIES (DIPTERA: SYRPHIDAE)

BY FRANCIS GILBERT*‡ AND JENNIFER OWEN†

**Department of Zoology, Nottingham University, Nottingham NG7 2RD; and*
†School of Life Sciences, Leicester Polytechnic, Leicester LE7 9SU and
66 Scraptoft Lane, Leicester LE5 1HU

SUMMARY

(1) We look for evidence of competition as indicated by population fluctuations and morphological relationships between species of hoverfly (Diptera: Syrphidae) in an urban community. Adult populations of this community have been monitored weekly for the past 15 years in a garden site using a Malaise trap.

(2) From analysing population fluctuations, there was little evidence of competitive interactions, except between species with predatory larvae. Even among these, highly specialized and moderately specialized predators do not appear to compete with one another; generalized species do appear to compete with one another, but not with other predators.

(3) Morphological features of the species played no detectable role in influencing population densities.

(4) These data suggest that hoverfly species respond largely independently to fluctuations in essential resources. For the urban habitat studied, at least, the idea of 'community' appears to be at best notional.

INTRODUCTION

Species that are morphologically similar tend also to have similar ecological requirements, and it is generally assumed that they compete. Therefore, the population sizes of morphologically close species are predicted to be inversely correlated, after allowing for temporally varying resources. We find little evidence for such inverse correlations in hoverflies (Diptera: Syrphidae), implying that some parts of conventional community theory are not applicable to this group.

This contributes to the recurring debate among ecologists concerning the nature of communities. There is no consensus on the importance of competition in promoting community structure, if such structure exists, or on the prevalence of density-dependent, density-vague (Strong 1986) or density-independent effects acting on population fluctuations (May 1984). There has been a recent emphasis on the idea that experimental manipulative techniques are the only methods able to resolve such controversies, but these are not always as reliable as is sometimes thought (Underwood 1986).

Current community theory predicts that competition will be stronger within than between feeding guilds, stronger between generalists than between specialists, and that morphologically similar species will also compete more strongly. Strong competition should be visible as reciprocal fluctuations in density.

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‡ Correspondence author.

We are concerned here and elsewhere (Owen & Gilbert 1989) with testing some of these predictions about the relationship between morphology, ecology and competition. We use a group of flower-visiting insects, the hoverflies (Diptera: Syrphidae), because several of the assumptions necessary for these tests have already been established. The most important of these are, firstly, that adult morphological features can be related directly to various aspects of species ecology; and second, that populations are generally at equilibrium levels. Using canonical correlation analysis (see Miles, Ricklefs & Travis 1987), a close relationship exists between morphology and foraging ecology in syrphids (Gilbert 1985a). Moreover, hoverfly populations are also not particularly variable even when compared with vertebrate populations (Owen & Gilbert 1989), according to the criteria of Connell & Sousa (1983) and Wolda (1983). Although a common belief is that insect populations are more variable in general than vertebrate ones, this is not borne out by actual evidence (Connell & Sousa 1983; but see Ostfeld 1988; Owen & Gilbert 1989). Some evidence from insect populations points to an astonishingly close tracking of the carrying capacity of the environment, i.e. a constant number of individuals per unit of resource (e.g. Oghushi & Sawada 1985). Experimental manipulation is not a realistic technique for assessing the role of competition amongst syrphids due to the mobility of adults; a novel indirect method is used here instead.

The analysis presented here parallels in part those for bird communities by James & Boecklen (1984) and Brawn, Boecklen & Balda (1987). These authors found that the most reasonable explanation for the patterns they observed is that species are responding independently of one another to resource distribution, giving an apparent but not real community stability; community 'structure' is only an epiphenomenon of the dominant process of the tracking of covarying resources by populations. We seek to compare these results with an insect community; reasons for regarding a taxonomic group of the hoverflies as a community have been given by Gilbert *et al.* (1985). James & Boecklen (1984) and Brawn, Boecklen & Balda (1987) among many others have made the same assumption (for birds), although this is not always justified (e.g. Schoener & Spiller 1987). We conclude that since morphological relationships appear to be influenced by competition in neither a bird nor an insect community, serious doubts must be cast upon the belief that competition structures communities.

The analysis presented here has ramifications not only as a test of community theory, but also has relevance for conservation approaches since it further justifies the great potential that hoverflies are believed to have for assessing the quality of habitats (Stubbs 1982; Speight 1986).

MATERIALS AND METHODS

Population densities

The data consist of population counts by J.O. and morphological measurements by F.S.G. Population data derive from an on-going long-term study (Owen 1981, 1983a, b; Owen & Owen 1975; Owen, Townes & Townes 1981) of the insect fauna of a suburban garden in Leicester, U.K. (National Grid Ref. SK624056, latitude 52°40′N). A Malaise trap has been run on the same site throughout the insect flight season (from April to October inclusive) since 1972. The trap is emptied weekly unless catches are so great that daily collection is necessary: data analysed here consist of fifteen annual totals of weekly trap catches of adult Syrphidae. We expect current competition to be evident in annual totals because phenological overlap between the common species analysed here is extensive: a future publication will assess within-year fluctuations in abundances. Nomenclature follows Stubbs & Falk (1983). Numbers are log-transformed in all analyses except the calculation of χ^2 similarity. This transformation $[\log_{10}(N+1)]$ stabilizes the variance (mean and variance of untransformed annual totals are correlated, $r=0{\cdot}78$, but uncorrelated when transformed, $r=0{\cdot}14$; for further discussion see Owen & Gilbert, 1989).

All species caught more than thirty times over the 15 years of collecting are included in the majority of the analysis, dividing the ninety-one recorded species into forty 'common' species and fifty-one 'rarer' species; the latter are only included where appropriate.

Morphological data

Most of the common species (the thirty-three commonest) have been measured in a standard manner for twenty-five variables: nearly all these data have been published (Gilbert 1985b), and we refer the reader to this paper for details of the methodology, sample sizes, variances and covariances. Ten variables are used here: wing length (WL), wing width (WW), head width (HW), thorax width (TW), hind tibia length (HTL), width of the second (T2), third (T3) and fourth (T4) tergites of the abdomen, and two measures of the proboscis, the length of the fulcrum (FL: an index of proboscis length, see Gilbert 1981) and the labellum length (the fleshy pad at the end of the proboscis, see Gilbert 1981). The measurements are changed to shape variables (Mosimann & James 1979) by the transformation $\log_{10}$ (measure) $-\log_{10}$ (HW), using head width as an index of general body size (justification, see below).

Looking for evidence of competition from population data

We perform three types of analysis. First, we look at patterns of density fluctuations to search for the effects of competition. We accomplish this by using 'χ^2 similarity', the similarity measure of correspondence analysis (Jöreskog, Klovan & Reyment 1976; Greenacre 1984). The advantage of using this measure is that it automatically allows for differences in overall abundance between species and between years, comparing profiles of species abundances through the years. The calculation used here is the similarity matrix relating species, which is a type of covariance:

$$r_{ij} = \Sigma_k \frac{P_{kj} - P_{k}.P_{\cdot j}}{\sqrt{P_{k}.P_{\cdot j}}} \quad \frac{P_{ki} - P_{k}.P_{\cdot i}}{\sqrt{P_{k}.P_{\cdot i}}}$$

where $i, j =$ species, $k =$ years, $P_{kj} =$ the probability that an observed individual belongs to species j and occurred in year k, and $P_k.P_{\cdot j}$ is a similar 'expected' probability, computed from the product of the marginal totals. This is equivalent to:

$$r_{ij} = \Sigma_k \sqrt{\frac{(\mathrm{O}_{kj} - \mathrm{E}_{kj})^2}{\mathrm{E}_{kj}}} \cdot \sqrt{\frac{(\mathrm{O}_{ki} - \mathrm{E}_{ki})^2}{\mathrm{E}_{ki}}}$$

where O_{kj} is the observed number of species j caught in year k, and E_{kj} is the corresponding 'expected' number obtained from the marginal totals. The measure is clearly the product of two χ^2 values, and takes large values when species abundances show complementary fluctuations across years.

We also calculate an alternative measure, 'χ^2 distance', defined by the following equation:

$$d_{ij}^2 = \Sigma_k \frac{1}{c_k} \left\{ \frac{x_{ik}}{r_i} - \frac{x_{jk}}{r_j} \right\}^2$$

where d_{ij}^2 is the χ^2 distance, c_k is the sum of all individuals caught in year k, r_i is the total number of individuals of species i caught over all k years, and x_{ik} is the number of individuals of species i caught in year k. This is the square of the 'χ^2 metric' of Legendre & Legendre (1983, p. 188), and very similar to the 'χ^2 distance' of Jongman, ter Braak & van Tongeren (1987, p. 152).

The null model

We test whether these χ^2 similarities and distances are different from random expectation by using a null model to generate an expected distribution. This should constitute a test of the effects of current competition on the abundances of species (cf. Colwell & Winkler 1984; Wilson 1987), since it disrupts any putative reciprocal density fluctuations between species. It is always possible that long-term relative abundances remain a product of past competitive forces.

The null model fits a two-way model based upon the marginal totals, and randomizes the residuals from the difference between observed and expected values (expressed as a proportion of the expected) by randomly exchanging pairs of rows or pairs of columns in the matrix of residuals. Each simulation makes forty exchanges of rows and forty of columns, i.e. the same as the number of species. After these exchanges, residuals are added back onto the expected values to generate a randomized matrix of numbers caught of forty species in 15 separate years: 100 random matrices are generated.

We test for competition within guilds in the following manner. For each subset (guild) tested, 100 mean similarities or distances are obtained from the random matrices, only including guild members, and the top five values compared with the observed mean value for the same subset of species. We accept as a significant result an observed mean value that lies in the top five of the 100 random mean values, since we predict that competitive interactions should lead to unusually large values of χ^2 similarity or distance because of the reciprocal fluctuations in density.

Another null model was also used, but the results are not presented here because the conclusions from it are very similar. This second null model randomly places all 43 359 individuals in the species × years matrix according to probabilities obtained from the marginal totals; the same significance test is used.

Competition within guilds

We analyse subsets of species classified either by adult feeding guilds (Gilbert 1985a) or by larval feeding guilds, essentially equivalent to taxonomic groups (see Stubbs & Falk 1983). Further analysis of the predatory species is possible, since species can be assigned to three groups (highly specialized, moderately specialized, and generalized): species were assigned where possible by Dr G. E. Rotheray (Royal Scottish Museum) on the basis of his extensive quantitative sampling of aphid colonies on plants (see also Owen & Gilbert 1989). Assignments to these guilds, and the taxonomic composition of the catch, are given in Table 1. We predict that if competitive effects can be found, they should be evident between generalists, and between generalists and other predators, rather than between specialists.

Morphological relationships between species

In the second type of analysis, we briefly analyse patterns in morphology using principal components analysis merely to display the main differences between species. We then compare positions of species in morphological space with those generated from a different type of random model, one that generates 'species' with random morphologies. Unlike many other random models (May 1984), we do not merely shuffle the recorded species in a random manner, but create 'species' according to an allometric model, thus avoiding the unreality of purely random morphologies (Simberloff 1983).

Thus the raw data, or data converted to shape variables, for each variable are regressed on a selected size variable. The size variable was chosen to be $\log_{10}$ (HW) from previous work on intraspecific variation in *Syrphus ribesii* (Gilbert 1985c). The regressions lead to a set of regression parameters from real data. Random matrices of morphological data are then constructed by the following procedure. We randomly choose a size either with a uniform probability between the observed maximum and minimum sizes, or by selecting a random deviation from the normal distribution of the untransformed HW data or from log-transformed HW data. We use two different distributions of head widths for these simulations: first, we use the mean and standard deviations from the thirty-three common species used in the morphological analyses in the rest of this paper; in addition, we use the distribution of head widths from more than 250 syrphid species from Britain and North America (see Fig. 1). Having obtained a size, the remaining nine (untransformed or shape) variables are constructed by predicting each variable from the observed regression equations, and randomly choosing a deviation from the estimated distribution at each predicted value. One hundred random matrices were constructed, and nearest-neighbour Euclidean distances compared with those from real species. Euclidean distances between species in morphological space were calculated using the GENSTAT computer package.

Morphology and population density

The final analyses look for relationships between morphology and density, and explicitly follows the protocol of James & Boecklen (1984), except that we use χ^2 similarity and χ^2 distance as our measure of the similarity in the profile of densities between any pair of species. The specific predictions and tests are detailed in the results section.

RESULTS

Patterns of densities

Overall patterns

χ^2 similarities and distances for all ninety-one species are dominated by very low values between rare species that were not recorded in most years; accordingly all further analyses are restricted to the forty commoner species. The distributions of χ^2 similarities or χ^2 distances between all forty species is very close to log-normal: we are uncertain whether this is a biologically interesting observation or not.

In the following account of our results, we refer to inferences from the analysis of χ^2 distances only where these differ from the results of analysing χ^2 similarities.

The distribution of χ^2 similarities from the random model is close to log-normal, systematically deviates from it, the first and third quartiles positively and the second and fourth negatively (cf. Sokal & Rohlf 1981: Box 6.1). The mean similarity between the forty species is not usually high, since seventy-two of the 100 random matrices had higher overall mean similarities. Because there is no difference in the distribution of similarities when any putative reciprocal density interactions are destroyed, we conclude that there is no evidence for the general occurrence of competitive interactions in the community. Thus, these data do not encourage the belief that there are many competitive interactions

TABLE 1. Classification of the commoner hoverfly species caught in a Leicester garden, including a classification by larval and adult feeding guilds as used in the analysis

	Guild membership*		
Subfamily, tribe, genus	Larval	Adult	Predator
Syrphinae			
Melanostomini			
1 *Baccha obscuripennis*	aphid	pollen	ms
2 *Melanostoma mellinum*	invert?	pollen-a	unk
3 *Melanostoma scalare*	invert?	pollen-a	unk
4 *Platycheirus ambiguus*	invert?	mixed PN	hs
5 *Platycheirus albimanus*	aphid	mixed PN	unk
6 *Platycheirus angustatus*	invert?	pollen-a	unk
7 *Platycheirus clypeatus*	invert?	pollen-a	unk
8 *Platycheirus manicatus*	invert?	mixed PN	ms
9 *Platycheirus peltatus*	invert?	mixed PN	ms
10 *Platycheirus scutatus*	aphid	mixed PN	ms
11 *Pyrophaena granditarsa*	invert?	pollen-a	unk
Paragini			
12 *Paragus tibialis*	aphid	pollen?	unk
Syrphini			
13 *Dasysyrphus albostriatus*	aphid	mixed PN	ms
14 *Epistrophe eligans*	aphid	mixed PN	ms
15 *Episyrphus balteatus*	aphid	pollen	g
16 *Leucozona lucorum*	aphid	mixed PN	ms
17 *Meliscaeva auricollis*	aphid	pollen	unk
18 *Metasyrphus corollae*	aphid	mixed PN	g
19 *Metasyrphus latifasciatus*	aphid	mixed PN	unk
20 *Metasyrphus luniger*	aphid	mixed PN	ms
21 *Scaeva pyrastri*	aphid	pollen	ms
22 *Sphaerophoria scripta*	aphid	mixed PN	ms
23 *Sphaerophoria menthastri*	aphid	mixed PN	ms
24 *Syrphus ribesii*	aphid	pollen	g
25 *Syrphus vitripennis*	aphid	pollen	ms

within these data; or, at least, they do not express themselves in reciprocal density fluctuations.

The positions of species and years in the space of the first two correspondence axes (Fig. 2), show that most species respond similarly to year-to-year variation, as indicated by the cluster of species and years in the lower left quadrant. The years 1975 and 1976 have different patterns of variation, mostly closely characterized by two species, *Metasyrphus corollae* and *Eumerus strigatus*, with high positive scores along CA1 and negative scores on CA2 (see Fig. 2): no biological reason for this can be advanced. Similarly the years 1977, 1982, 1985 and 1986 are different, with variation in these years being characterized by species such as *Scaeva pyrastri*, *Meliscaeva auricollis*, and *Episyrphus balteatus*, all pollen specialists.

Possible larval competition: tribal analyses

The overall analysis may obscure patterns within subsets of the data. We therefore analysed tribal groupings, which are predominantly expected to detect effects of larval competition since larval feeding behaviour within tribes is generally more similar than adult feeding behaviour. We use here the traditional tribal boundaries, although these

TABLE 1 (*continued*)

Subfamily, tribe, genus	Guild membership* Larval	Adult	Predator
Eristalinae			
Brachyopini			
26 *Cheilosia vernalis*	plant	mixed PN	—
27 *Rhingia campestris*	sapro	nectar	—
Chrysogasterini			
28 *Neoascia podagrica*	sapro	mixed NP?	—
Eristalini			
29 *Eristalis arbustorum*	sapro	mixed NP	—
30 *Eristalis interrupta*	sapro	mixed NP	—
31 *Eristalis intricarius*	sapro	mixed NP	—
32 *Eristalis pertinax*	sapro	mixed NP	—
33 *Eristalis tenax*	sapro	mixed NP	—
34 *Helophilus pendulus*	sapro	mixed NP	—
Merodontini			
35 *Eumerus strigatus*	plant	mixed PN	—
36 *Eumerus tuberculatus*	plant	mixed PN	—
37 *Merodon equestris*	plant	mixed PN	—
Pipizini†			
38 *Neocnemodon vitripennis*	aphid	pollen	hs
39 *Pipiza noctiluca*	aphid	pollen	ms
Xylotini			
40 *Syritta pipiens*	sapro	mixed PN	—

* invert = predatory, probably prefering aphids, but feeding on other invertebrates if necessary, often in the leaf-litter layer; aphid = predatory, feeding only on aphids; sapro = saprophagous; plant = phytophagous; pollen = feeding primarily on pollen; pollen-a = feeding primarily on anemophilous pollen; mixed PN = taking more pollen than nectar in the diet; mixed NP = taking more nectar than pollen in the diet; nectar = feeding primarily on nectar; hs = highly specialized; ms = moderately specialized; g = generalized; unk = unknown.

† The tribe Pipizini is included here by recent catalogues, but correctly belongs to the Syrphinae (Rotheray & Gilbert 1989).

have recently been modified (see Rotheray & Gilbert 1989). Three tribes are well represented among the species of the garden, the Syrphini, the Melanostomini, and the Eristalini (see Table 1). The test for competition within these subsets of the data consists of contrasting the mean χ^2 similarity for these species against 100 means for randomly created matrices (see Methods).

The Syrphini have aphid-specific predatory larvae which might be expected to compete for food since aphid colonies are frequently obliterated by their attentions. However, the observed mean similarity was exceeded in magnitude by thirty-five of 100 random mean, and we conclude that there is no evidence for competition within this tribe from these data.

The Melanostomini is an interesting tribe, most of whose species have larvae that are probably generalized predators in the leaf litter (although this has not yet been proven). The tribe forms the largest grouping amongst the forty commonest species of the garden. The observed mean similarity has a high value, with only nine of the random means being larger. Although we cannot take this as a significant result, we believe that it reflects the generalized feeding habits of most of this group, even though most species cannot be

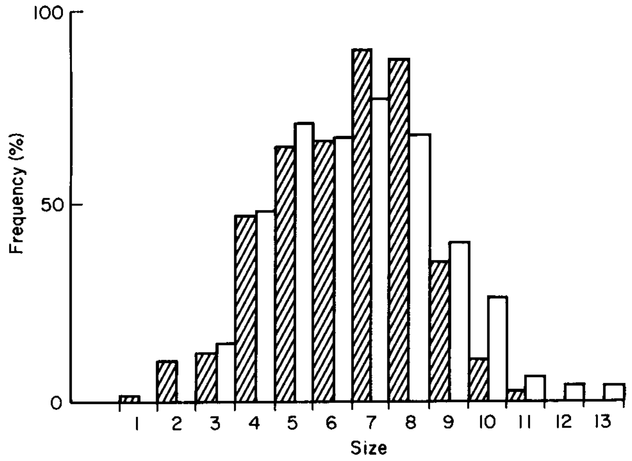

FIG. 1. Frequency distribution of the sizes (head width) of Holarctic Syrphidae. Each of the 250+ species has separate head width data for each sex where available: raw data in 0·5-mm intervals (□); log-transformed data in intervals of 0·08 (■). Neither distribution deviates significantly from a normal distribution using the Kolmogorov–Smirnov test: for raw data, $D = 0{\cdot}0374$, N.S.; log-transformed data, $D = 0{\cdot}0561$, N.S.

conclusively categorized as generalist predators due to lack of knowledge (cf. below, generalist predators).

Finally the Eristalini, with aquatic filter-feeding larvae, also show no evidence for competitive interactions, with the observed mean similarity being exceeded by seventeen of the 100 random means.

Possible adult competition: feeding guilds

Two main feeding guilds are present in the garden, the pollen specialists, and mixed-diet feeders; species taking mainly nectar (a third guild: see Table 1) are few. Neither guild shows any evidence for unusually high mean similarities. For all pollen feeders, forty random means were higher than the observed; for those with a mixed diet, sixty-seven were higher. Among the pollen specialists there exists a subgroup of species feeding on anemophilous pollens (cf. van der Goot & Grabandt 1970). There is no evidence that these species compete, since their mean similarity was exceeded by sixteen random mean values.

Effect of the degree of specialization in predators

We predict that generalists should be more likely to compete with one another and with other predators than moderate or narrow specialists amongst themselves.

There are only two species which we can definitely classify as highly specialized. There is therefore only one observed χ^2 similarity, which is about half-way between the smallest and the largest recorded similarity. It is not remarkably large, since sixty-two random means exceed it.

The mean χ^2 similarity amongst moderate specialists is also not remarkably large, with seventy-three random means exceeding it.

Amongst the three species of generalists, however, a different situation is apparent: here the mean similarity is greater than the third largest mean from 100 random matrices. It

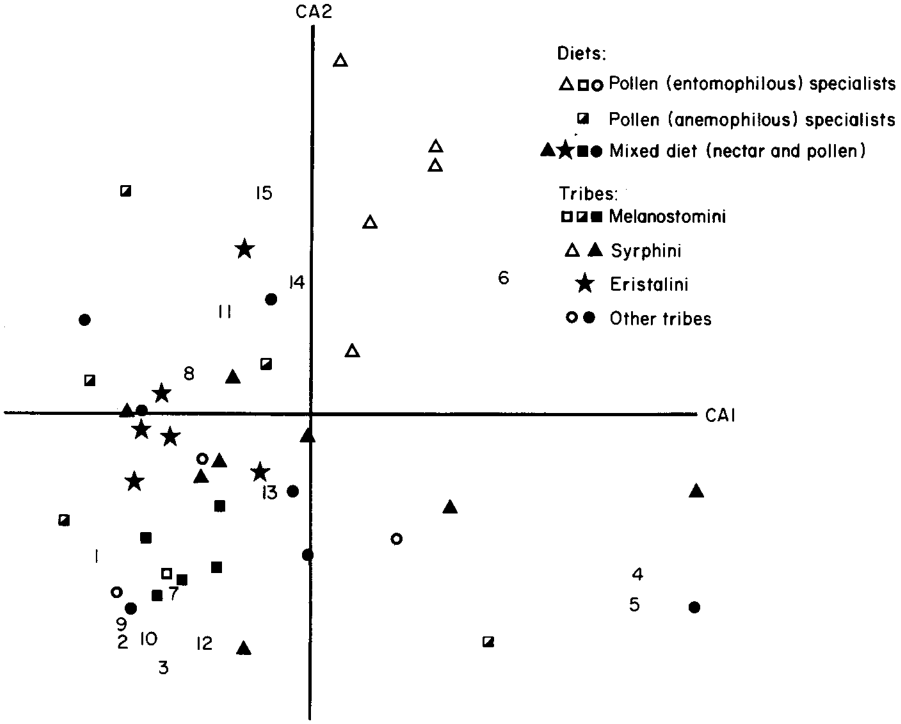

FIG. 2. Correspondence analysis of the annual abundances of Leicester hoverflies over 15 years. Positions of the forty common species are plotted in the space of the first two correspondence axes, which contain 48% of the total similarity. Positions of the 15 years (1972–86) are also plotted as numbers 1–15 to show how species positions are determined by their abundances in each year.

seems unlikely that it is this large by chance alone. This result is, however, not supported by the analysis of χ^2 distances.

The mean similarity between the three generalists and all other predators (whose degree of specialization is known) is rather small, being exceeded by eighty-three of the random means.

We conclude that there is no evidence for competition within guilds of highly or moderately specialized predator, or between the generalist predators and the rest. We also conclude that competition is possibly evident within the guild of generalist predators. This is possibly supported by the high ($P < 0{\cdot}10$) mean χ^2 similarity of the Melanostomini, most of whose members are probably generalized predators, although we cannot definitely assign them to this category.

Morphological relationships

Mean values for each species were used in a Principal Components Analysis of the covariance matrix to display the species in the morphological space of the size and shape variables. Figure 3 shows the first two axes which account for 74% of the variance. PCA1 (53% of the variance) is mainly reflecting the relatively larger wings of smaller species, while PCA2 mainly records the shape of the proboscis. As in a previous analysis (Gilbert 1985b), *Baccha* and *Rhingia* are outliers due to their remarkably different shapes.

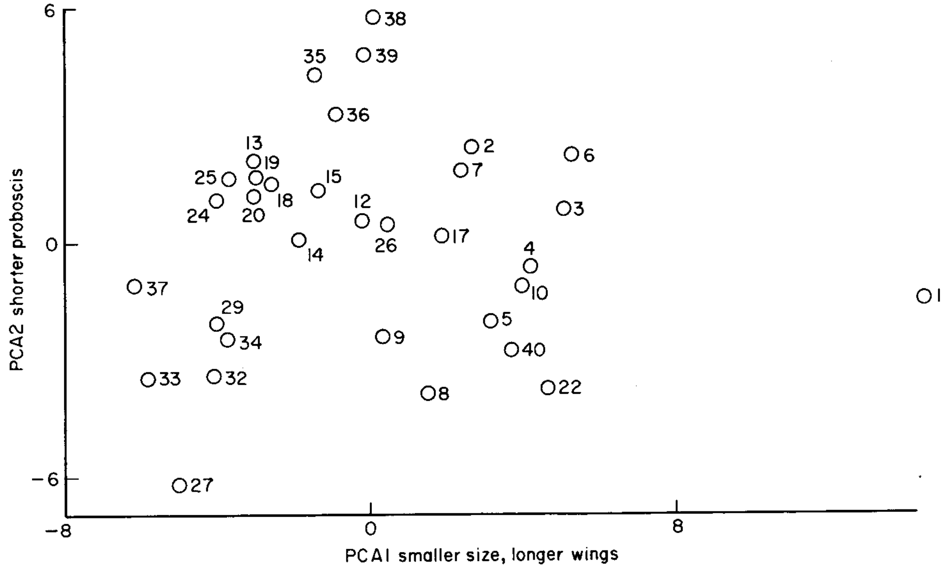

FIG. 3. Plot of the first two axes of a principal components analysis of size and shape variables of the thirty-three commonest hoverflies of the garden. Interpretation of the axes is based on the correlations between the original variables and the loadings of the species on the principal axes. These two axes explain 74% of the variance in the original data.

Euclidean distances between species were calculated in the space of the ten variables, and the mean nearest-neighbour distance found. This was compared to similar distances calculated for 100 communities composed of thirty-three species with random morphologies chosen to conform with observed allometric relationships (Table 2). In most comparisons, species with randomly chosen sizes are either not significantly nearer or further apart in morphological space than observed species, or they are significantly *further* apart. Niche theory and the theory of species packing predicts that competition forces species apart in morphological space, and therefore that the observed mean nearest-neighbour distance will be greater than randomly generated ones. Since the observation is directly contrary to the prediction, there is certainly no evidence for competition spacing species further apart than they would otherwise be.

Relationships between morphology and density

Is there a correlation between morphological distance and density?

We would expect species close together in morphological space to show reciprocal density fluctuations, and therefore large χ^2 similarities and distances, if we accept current community theory. In fact, these variables are uncorrelated (e.g. for χ^2 similarities and Euclidean distances, $r = -0{\cdot}085$, $n = 33$ because of interdependencies, N.S.). Perhaps the expected negative relationship is obscured by considering all pairs of species. We therefore consider only nearest-neighbour distances (NND); for the twenty-four pairs of nearest neighbours (eight pairs are mutual nearest-neighbours) there is no association (for χ^2 similarities, $r = -0{\cdot}32$, N.S.; for χ^2 distances, $r = -0{\cdot}10$, N.S.).

Do common species influence their nearest neighbours more than rare species? If so, we expect a positive correlation between mean density and NND: actually the relationship is significant but negative ($r = -0{\cdot}35$, $n = 33$, $P = 0{\cdot}05$), and explains very little of the

TABLE 2. Comparison between observed nearest-neighbour distances (NND) in morphological space between hoverflies in a garden community, and those generated from a random model

	Average of mean NND for 100 simulated communities ±S.E.	
	Leicester†	Holarctic†
(a) Raw data		
Observed mean NND = 0·148 ($n=32$)		
Random mean NND*		
Model I	0·175 ± 0·029 (N.S.)	0·264 ± 0·041 (**)
Model II	0·173 ± 0·025 (N.S.)	0·322 ± 0·051 (***)
Model III	0·209 ± 0·041 (N.S.)	0·214 ± 0·042 (N.S.)
Model IV	0·169 ± 0·034 (N.S.)	0·183 ± 0·031 (N.S.)
(b) Shape variables		
Observed mean NND = 1·233 ($n=32$)		
Random mean NND		
Model I	1·95 ± 0·22 (**)	2·78 ± 0·32 (***)
Model II	1·77 ± 0·21 (*)	2·71 ± 0·31 (***)
Model III	1·78 ± 0·35 (N.S.)	2·00 ± 0·40 (*)
Model IV	1·48 ± 0·21 (N.S.)	1·75 ± 0·23 (*)

* Four random models are used: I = random sizes drawn from a uniform distribution between the maximum and minimum head widths; II = random sizes drawn from a uniform distribution between log(maximum head width) and log(minimum head width); III = random sizes drawn from a normal distribution centred on the mean head width and with the observed standard deviation; IV = random sizes drawn from a log-normal distribution centred on the mean of log(head width), and with the observed standard deviation.

† Random sizes are chosen from two sets of the four observed parameters (i.e. the mean, standard deviation, maximum and minimum head widths). 'Leicester' means that these parameters are obtained from the set of thirty-three common species of the garden. 'Holarctic' means that the parameters derive from an extensive study of the morphometrics of more than 250 syrphid species from Europe and North America.

‡ Significance assessed by t-tests for a single mean compared with an estimated distribution of mean values. All tests are two-tailed. (N.S.) = non-significant; (*) = significant at the 5% level; (**) = significant at the 1% level; (***) = significant at the 0·1% level.

variance (12%). Perhaps species closer in morphological space induce a greater variance in density; if so, we expect a negative correlation between NND and the variance in density, but they are actually uncorrelated ($r=-0{\cdot}12$, $n=33$, N.S.).

Does position in morphological space matter?

Species with extreme morphologies are specialists and would be expected to be at lower densities (cf. Owen & Gilbert 1989) than species with more generalized morphologies. This prediction can be assessed by correlating mean density with distance from the centroid of morphological space: there is no such correlation ($r=-0{\cdot}22$, $n=33$, N.S.). We also expect specialists to fluctuate more in density; however, no correlation exists between distance from the centroid and variance in density ($r=-0{\cdot}22$, $n=33$, N.S.).

To estimate the effects of diffuse competition, we look at the similarity matrix of morphologies generated by GENSTAT using Euclidean distances. Species with many near neighbours are expected to have lower and/or more variable densities. For each species, we count the number of other species with similarities greater than 0·95, and correlate this with mean and variance in density: there is no correlation with either the mean ($r=0{\cdot}28$, $n=33$, $P=0{\cdot}05$ with a one-tailed test but in the wrong direction, positive not negative) or the variance ($r=0{\cdot}12$, $n=33$, N.S.).

Having failed to find any relationship between species, perhaps there is a cumulative density effect. Species with a greater density of near-neighbour individuals are expected to have lower and/or more variable densities. For each species, we add together the densities of all species morphologically more similar than 0·95 according to the similarity matrix generated from Euclidean distances by GENSTAT, and correlate this with the mean and variance in density: however, neither show a significant association (with mean density, $r=0{\cdot}29$, $n=33$, $P=0{\cdot}05$ in a one-tailed test but is positive instead of negative; with variance in density, $r=0{\cdot}15$, N.S.).

DISCUSSION

It is remarkable that there is an almost total absence of any relationship between community and morphological patterns in these data; such a result has now been demonstrated in two studies, from both bird and insect communities. Hoverfly communities appear to have some sort of 'structure' in the sense that relative abundances are correlated between years, i.e. rank abundances are preserved more or less from year to year (Owen & Gilbert 1989). However, as shown herein, any community structure that does exist in this community seems to have little to do with interspecific competition, either larval (except possibly in generalist predators) or adult, and is not affected by morphology.

This study has found no evidence for morphological character displacement when comparing real species with randomly constructed ones with realistic morphologies. Ricklefs & Travis (1980) also generated random morphologies, but these were without reference to allometric constraints and were therefore likely to be unrealistic (Simberloff 1983). Most other authors have selected random subsets of species, usually birds, from a species pool (Ricklefs & Travis 1980; Bowers & Brown 1982; Case, Faaborg & Sidell 1983; Travis & Ricklefs 1983; Schoener 1984; Brown & Bowers 1985; Moulton & Pimm 1986, 1987), and have sometimes found significant overdispersion. Using similar selection techniques, Gilbert *et al.* (1985) found significant overdispersion in a hoverfly community or ancient woodland, but not in two urban habitats. While the urban community studied here clearly is not structured by morphologically mediated competition, it is possible that a similar long-term monitoring of densities in ancient woodland would reveal a different story. No data exist to test this hypothesis.

All our results support the conclusion of James & Boecklen (1984) and of Brawn, Boecklen & Balda (1987) that species are tracking resources independently of each other. This 'species-constellation' idea (Kikkawa 1977; Birch 1979; den Boer 1980) reiterates an old concept from natural history, that related species are *more* likely to covary in their use of resources and in population density than are unrelated species. The similarity in density fluctuations between various groupings of syrphid species point unequivocally to their tracking of covarying or common resources. One clear example of this is the parallel fluctuations of the group of anemophilous-pollen specialists, the *Melanostoma–Platycheirus* group (van der Goot & Grabandt 1970; Stelleman, 1978: cf. Fig. 3).

It is interesting that the only indication of competitive relationships among the data come from predators. These syrphid larvae are often voracious predators that can easily wipe out colonies of aphids; perhaps one might expect competition to be important in this group. Even more interesting are the differences between the various degrees of feeding specialization within the predators; only generalized species show evidence of reciprocal fluctuations in abundance. This supports the idea that, at least in part, the selective pressure for specialization involves an escape from competition; we know that evolution has overwhelmingly occurred in a direction from generalist feeders to specialized ones (Rotheray & Gilbert 1989; Gilbert 1990).

Hoverflies share similarities in behaviour and interspecific relationships with bumblebees, in that they show flower constancy, forage in a very similar manner, and visit flowers whose corolla depth matches their proboscis length (Gilbert 1981). It has been stated that bumblebee communities are structured by competitive relationships acting via proboscis length (e.g. Heinrich 1979), permitting only three or four species to coexist in any one habitat. These hypotheses are built upon experimental demonstrations of competition mediated by proboscis length (Inouye 1978; Bowers 1985). However, there exist more diverse bumblebee communities than are allowed under this hypothesis (e.g. Ranta & Vepsäläinen 1981), and these are interpreted as communities not structured by competition acting via proboscis length. The very diverse hoverfly communities reported here, which are common to most habitats, appear to lack detectable 'structure' in this classical sense. It is possible that only in relatively stable habitats do syrphid communities display such patterns (Gilbert *et al.* 1985).

What then does the concept of 'community' mean? One can take an extreme Clementsian view, a 'holist vision' (see Harper 1980), and regard a community as an organized whole more than the sum of its individual parts, showing emergent properties (Salt 1979), and implying the ontological emergence of a community level of biotic organization (see review by Hoffman 1979). Such a view is hard to maintain in the face of the results reported here and elsewhere. Syrphid communities show similarities between years only in the long-term maintenance of rank abundances. The evidence points to resource-based reasons for this, rather than competitive relationships. We believe therefore that any 'structure' is a biological epiphenomenon, a statistical abstraction, a descriptive convention without true emergent properties but only collective ones, wholly referable in its properties to those of the constituent species, populations, and individuals. Thus, we believe that animal ecology is learning what botanists learnt many decades ago (see review by Jackson 1981), and lean to the view that at least some communities of syrphids are merely coincidences of species in space and time.

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REFERENCES

Birch, L. C. (1979). The effect of species of animals which share common resources on one another's distribution and abundance. *Fortshritte der Zoologie*, **25**, 197–222.

den Boer, P. J. (1980). Exclusion or coexistence, and the taxonomic or ecological relationships between species. *Netherlands Journal of Zoology*, **30**, 278–306.

Bowers, M. A. (1985). Experimental analysis of competition between two species of bumblebees (Hymenoptera; Apidae). *Oecologia*, **67**, 224–230.

Bowers, M. A. & Brown, J. H. (1982). Body size and coexistence in desert rodents: chance or community structure? *Ecology*, **63**, 391–400.

Brawn, J. D., Boecklen, W. D. & Balda, R. P. (1987). Investigations of density interactions among breeding birds in ponderosa pine forests: correlative and experimental evidence. *Oecologia*, **72**, 348–357.

Brown, J. H. & Bowers, M. A. (1985). Community organisation in hummingbirds: relationships between morphology and ecology. *Auk*, **102**, 251–269.

Case, T. J., Faaborg, J. & Sidell, R. (1983). The role of body size in the assembly of West Indian bird communities. *Evolution*, **37**, 1062–1074.

Colwell, R. K. & Winkler, D. W. (1984). A null model for null models in biogeography. *Ecological Communities: Conceptual Issues and the Evidence* (Ed. by D. R. Strong *et al.*), pp. 344–359. Princeton University Press, Princeton.

Connell, J. H. & Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. *American Naturalist*, **121**, 789–824.

Gilbert, F. A. (1981). Foraging ecology of hoverflies (Diptera, Syrphidae): morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecological Entomology*, **6**, 245–262.

Gilbert, F. S. (1985a). Ecomorphological relationships in hoverflies (Diptera, Syrphidae). *Proceedings of the Royal Society of London B*, **224**, 91–105.

Gilbert, F. S. (1985b). Morphometric patterns in hoverflies (Diptera, Syrphidae). *Proceedings of the Royal Society of London B*, **224**, 79–90.

Gilbert, F. S. (1985c). Size and shape in *Syrphus ribesii* (Diptera, Syrphidae). *Proceedings of the Royal Society of London B*, **224**, 107–114.

Gilbert, F. S. (1990). Size and phylogeny in the specialisation of insect predators. *The Evolution and Coordination of Insect Life Cycles* (Ed. by F. S. Gilbert) (in press). Springer Verlag, London.

Gilbert, F. S., Harding, E. F., Line, J. M. & Perry, I. (1985). Morphological approaches to community structure in hoverflies (Diptera, Syrphidae). *Proceedings of the Royal Society of London B*, **224**, 115–130.

van der Goot, V. & Grabandt, R. A. J. (1970). Some species of the genera *Melanostoma*, *Platycheirus* and *Pyrophaena* (Diptera, Syrphidae) and their relation to flowers. *Entomologische Bericht, Amsterdam*, **30**, 135–143.

Greenacre, M. J. (1984). *Theory and Applications of Correspondence Analysis*. Academic Press, London.

Harper, J. L. (1980). Plant demography and ecological theory. *Oikos*, **35**, 244–253.

Heinrich, B. (1979). *Bumblebee Economics*. Harvard University Press.

Hoffman, A. (1979). Community paleoecology as an epiphenomenal science. *Paleobiology*, **5**, 357–379.

Inouye, D. W. (1978). Resource partitioning in bumblebees: experimental studies of foraging behaviour. *Ecology*, **59**, 672–678.

Jackson, J. B. C. (1981). Interspecific competition and species' distributions: the ghosts of theories and data past. *American Zoologist*, **21**, 889–901.

James, F. C. & Boecklen, W. J. (1984). Interspecific morphological relationships and the densities of birds. *Ecological Communities: Conceptual Issues and the Evidence* (Ed. by D. R. Strong *et al.*), pp. 458–477. Princeton University Press, Princeton.

Jongman, R. H. G., ter Braak, C. J. F. & van Tongeren, O. F. R. (1987). *Data Analysis in Community and Landscape Ecology*. Pudoc, Wageningen.

Jöreskog, K. G., Klovan, J. E. & Reyment, R. A. (1976). Geological factor analysis. *Methods in Geomathematics 1*. Elsevier, Amsterdam.

Kikkawa, J. (1977). Ecological paradoxes. *Australian Journal of Ecology*, **2**, 121–136.

Legendre, L. & Legendre, P. (1983). *Numerical Ecology*. Elsevier, Amsterdam.

May, R. M. (1984). An overview: real and apparent patterns in community structure. *Ecological Communities: Conceptual Issues and the Evidence* (Ed. by D. R. Strong *et al.*), pp. 3–16. Princeton University Press, Princeton.

Miles, D. B., Ricklefs, R. E. & Travis, J. (1987). Concordance of ecomorphological relationships in three assemblages of passerine birds. *American Naturalist*, **129**, 347–364.

Mosimann, J. E. & James, F. C. (1979). New statistical methods for allometry with application to Florida Red-winged Blackbirds. *Evolution*, **33**, 444–459.

Moulton, M. P. & Pimm, S. L. (1986). The extent of competition in shaping an introduced avifauna. *Community Ecology* (Ed. by J. M. Daimond & T. J. Case), pp. 80–97. Harper Row, London.

Moulton, M. P. & Pimm, S. L. (1987). Morphological assortment in introduced Hawaiian passerines. *Evolutionary Ecology*, **1**, 113–124.

Ohgushi, T. & Sawada, H. (1985). Population equilibrium with respect to available food resource and its behavioural basis in an herbivorous lady beetle, *Henosepilachna niponica*. *Journal of Animal Ecology*, **54**, 781–796.

Ostfeld, R. S. (1988). Fluctuations and constancy in populations of small rodents. *American Naturalist*, **131**, 445–452.

Owen, J. (1981). Trophic variety and abundance of hoverflies (Diptera, Syrphidae) in an English suburban garden. *Holarctic Ecology*, **4,** 221–228.

Owen, J. (1983a). *Garden Life*. Chatto & Windus, London.

Owen, J. (1983b). Effect of contrived plant diversity and permanent succession on insects in English suburban gardens. *Urban Entomology: Interdisciplinary Perspectives* (Ed. by G. W. Frankie & C. S. Koehler). Praeger, New York.

Owen, J. & Gilbert, F. S. (1989). On the abundance of hoverflies (Diptera, Syrphidae). *Oikos* (in press).

Owen, J. & Owen, D. F. (1975). Suburban gardens: England's most important nature reserves. *Environmental Conservation*, **2,** 53–59.

Owen, J., Townes, H. & Townes, M. (1981). Species diversity of Ichneumonidae and Serphidae (Ichneumonidae) in an English suburban garden. *Biological Journal of the Linnean Society*, **16,** 315–336.

Ranta, E. & Vepsäläinen, K. (1981). Why are there so many species? Spatio-temporal heterogeneity and northern bumblebee communities. *Oikos*, **36,** 28–34.

Ricklefs, R. E. & Travis, J. (1980). A morphological approach to the study of avian community organisation. *Auk*, **97,** 321–338.

Rotheray, G. E. & Gilbert, F. S. (1989). The phylogeny and systematics of the tribe Syrphinae (Diptera, Syrphidae) according to larval morphology. *Zoological Journal of the Linnean Society*, **95,** 27–70.

Salt, G. W. (1979). A comment on the use of the term *emergent properties*. *American Naturalist*, **113,** 145–148.

Schoener, T. W. (1984). Size differences among sympatric bird-eating hawks: a world-wide survey. *Ecological Communities: Conceptual Issues and the Evidence* (Ed. by D. R. Strong *et al.*), pp. 254–271. Princeton University Press, Princeton.

Schoener, T. W. & Spiller, D. A. (1987). Effects of lizards on spider populations: manipulative reconstruction of a natural experiment. *Science*, **236,** 949–952.

Simberloff, D. (1983). Biogeography: the unification and maturation of a science. *Perspectives in Ornithology* (Ed. by A. H. Brush & G. A. Clark), pp. 411–455. Cambridge University Press, Cambridge.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. 2nd edn. Freeman & Co., San Fransisco.

Speight, M. C. D. (1986). Criteria for the selection of insects to be used as bio-indicators in nature conservation research. *Proceedings of the 3rd European Congress of Entomology, Amsterdam*, **3,** 485–488.

Stelleman, P. (1978). The possible role of insect visits in pollination of reputedly anemophilous plants, exemplified by *Plantago lanceolata* and syrphid flies. *Pollination of Flowers by Insects* (Ed. by A. J. Richards). Linnean Society Symposium 6.

Strong, D. R. (1986). Density vagueness: abiding the variance in the demography of real populations. *Community Ecology* (Ed. by T. J. Case & J. M. Diamond), pp. 257-268. Harper Row, London.

Stubbs, A. E. (1982). Hoverflies as primary woodland indicators with reference to Wharncliffe Wood. *Sorby Record*, **20,** 62–67.

Stubbs, A. E. & Falk, S. (1983). *British Hoverflies: an Identification Guide*. British Entomological & Natural History Society, London.

Travis, J. & Ricklefs, R. E. (1983). A morphological comparison of island and mainland assemblages of neotropical birds. *Oikos*, **41,** 434–441.

Underwood, A. D. (1986). The analysis of competition by field experiments. *Community Ecology: Pattern and Process* (Ed. by D. J. Anderson & J. Kikkawa), pp. 240–268. Blackwell Scientific Publications, Oxford.

Wilson, J. B. (1987). Methods for detecting non-randomness in species co-occurrences: a contribution. *Oecologia*, **73,** 579–582.

Wolda, H. (1983). 'Long-term' stability of tropical insect populations. *Research in Population Ecology, Supplement*, **3,** 112–136.

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APPENDIX 1

Annual totals for trap catches of the forty species of hoverfly used in the analysis. They were trapped at Leicester over the period 1972–86.

Species	Annual total catch for each year 1972–86									
B. obscuripennis	9	12	40	5	13	5	22	13	4	5
	5	4	9	5	3					
M. mellinum	200	249	112	65	47	2	266	805	98	35
	1159	46	179	265	305					
M. scalare	72	46	98	20	10	0	89	163	55	66
	120	16	11	78	37					
P. ambiguus	74	107	60	60	15	11	21	8	8	1
	38	0	4	3	13					
P. albimanus	250	465	789	402	129	100	1238	452	249	284
	205	182	111	439	95					
P. angustatus	26	55	45	10	3	4	68	14	64	15
	44	10	32	21	16					
P. clypeatus	53	116	136	393	105	3	401	286	16	19
	650	35	28	16	85					
P. manicatus	40	54	6	18	49	6	54	22	99	16
	19	11	3	15	5					
P. peltatus	29	38	20	47	29	1	14	72	44	9
	25	22	5	11	7					
P. scutatus	205	618	358	407	327	243	1155	243	169	89
	98	108	133	124	77					
P. granditarsa	0	7	2	16	0	0	0	0	0	1
	3	3	0	0	0					
P. tibialis	1	19	5	19	27	1	13	5	1	0
	16	8	8	5	0					
D. albostriatus	4	12	18	4	12	7	13	7	10	5
	3	8	5	21	5					
E. eligans	10	11	17	12	33	26	37	7	16	3
	21	2	13	7	8					
E. balteatus	82	126	103	746	402	1143	459	299	26	12
	473	20	177	1073	435					
L. lucorum	0	6	1	1	10	3	0	0	3	0
	4	0	0	1	0					
M. auricollis	0	1	3	5	1	55	16	10	4	0
	4	4	0	4	1					
M. coroillae	17	50	165	2580	1359	425	114	272	66	73
	414	58	221	191	70					
M. latifasciatus	3	3	1	10	0	0	8	42	3	19
	13	13	6	0	2					
M. luniger	56	60	119	52	38	54	123	102	20	16
	14	11	35	64	6					
S. pyrastri	2	0	2	2	0	7	1	2	0	0
	0	1	2	15	3					
S. scripta	8	32	28	96	40	52	356	86	27	23
	65	81	404	270	15					
S. menthastri	3	2	9	15	1	1	33	1	1	1
	1	0	0	1	0					
S. ribesii	5	77	16	316	17	77	260	130	51	19
	20	45	10	364	19					
S. vitripennis	2	1	6	40	21	33	36	52	6	2
	7	4	9	55	26					

Species	Annual total catch for each year 1972–86									
C. vernalis	0	0	0	0	0	0	3	0	8	39
	68	11	7	3	1					
R. campestris	10	23	21	15	0	0	12	24	21	19
	23	15	11	44	5					
N. podagrica	6	34	4	9	2	0	3	2	1	2
	9	0	1	2	0					
E. arbustorum	29	362	10	75	21	53	336	74	69	11
	164	62	144	117	14					
E. interrupta	0	8	0	0	2	1	1	2	4	2
	8	9	9	10	0					
E. intricarius	0	5	1	1	1	1	6	7	2	2
	2	2	5	4	0					
E. pertinax	11	6	10	19	1	10	28	13	12	3
	5	2	5	69	12					
E. tenax	20	63	20	12	6	31	50	13	9	2
	10	4	11	33	11					
H. pendulus	7	80	9	72	8	16	53	5	9	18
	37	35	26	57	6					
E. strigatus	18	34	34	351	217	24	40	11	7	11
	36	6	22	4	2					
E. tuberculatus	5	118	58	145	68	15	12	8	3	3
	78	235	119	33	33					
M. equestris	10	25	32	34	66	32	48	49	42	13
	68	34	75	51	100					
N. vitripennis	8	25	9	8	3	0	30	9	1	0
	0	1	3	4	3					
P. noctiluca	5	14	6	8	10	3	7	1	18	3
	27	2	4	4	1					
S. pipiens	35	146	106	240	287	146	610	155	56	32
	273	151	178	39	19					

APPENDIX 2

Species means for morphometric data on hoverflies as used in the analysis; all except 'head width' are converted to shape variables by the method of Mosimann & James (1979) [see text].

Abbreviations (each refers to log[x] − log[HW], except HW itself): WL = wing length; WW = wing width; HW = head width; TW = thorax width; HTL = hind tibia length; FL = fulcrum length; LL = labellum length; T2, T3, T4 = widths of tergites 2, 3, 4, respectively. Data given in the table are multiplied by ten for convenience. Sample sizes and variances for nearly all the species included here are given in Gilbert (1985b).

Species	WL	WW	HW	TW	HTL	FL
B. obscuripennis	6·30	0·67	2·43	−1·94	−0·20	−4·37
M. mellinum	4·96	0·38	3·14	−1·29	−0·99	−4·81
M. scalare	5·29	0·43	3·46	−1·37	−1·08	−4·77
P. albimanus	4·64	−0·32	3·80	−1·32	−1·47	−3·35
P. ambiguus	4·38	−0·44	3·42	−1·69	−1·99	−3·93
P. angustatus	5·07	0·42	2·76	−1·83	−1·03	−5·06
P. clypeatus	5·04	0·27	3·62	−1·44	−1·04	−4·75
P. manicatus	4·80	−0·33	4·42	−1·24	−1·44	−2·44
P. peltatus	4·83	−0·20	4·31	−1·11	−1·28	−2·82
P. scutatus	4·74	−0·27	3·38	−1·48	−1·54	−3·61
P. tibialis	3·81	−1·00	2·76	−1·09	−1·73	−3·32
D. albostriatus	4·35	−0·59	5·31	−1·28	−1·48	−5·10
E. eligans	4·18	−1·03	5·66	−1·11	−1·78	−4·83
E. balteatus	5·19	0·03	4·84	−0·95	−0·88	−4·67
M. auricollis	5·18	−0·17	4·28	−0·98	−1·00	−4·41
M. corollae	4·36	−0·20	4·83	−1·25	−1·31	−4·45
M. latifasciatus	4·18	−0·23	4·87	−1·09	−1·37	−4·46
M. luniger	4·42	−0·19	5·05	−1·16	−1·47	−4·44
S. scripta	4·33	−0·96	3·75	−1·55	−0·65	−2·92
S. ribesii	4·50	−0·60	5·63	−0·91	−1·24	−4·70
S. vitripennis	4·47	−0·60	5·35	−1·04	−1·39	−4·82
C. vernalis	4·15	−0·36	3·28	−0·36	−1·41	−3·74
R. campestris	4·35	−0·47	5·05	−0·75	−1·57	−0·46
E. arbustorum	3·75	−0·93	5·90	−0·96	−1·54	−3·54
E. pertinax	3·92	−1·10	6·84	−1·00	−1·23	−3·64
E. tenax	3·67	−0·99	7·23	−0·97	−1·26	−3·48
H. pendulus	3·86	−0·99	5·79	−0·94	−1·02	−3·33
E. strigatus	3·79	−0·33	3·96	−0·95	−1·89	−5·70
E. tuberculatus	3·45	−0·45	3·46	−1·03	−2·00	−4·95
M. equestris	3·69	−0·52	6·39	−0·55	−0·94	−3·75
N. vitripennis	4·44	0·21	2·70	−1·33	−1·80	−5·71
P. noctiluca	3·83	−0·49	3·50	−0·90	−1·77	−6·02
S. pipiens	4·43	−0·34	3·22	−0·97	−0·34	−2·89

Species	LL	T2	T3	T4
B. obscuripennis	−5·11	−6·20	−2·56	−1·16
M. mellinum	−4·94	−0·49	−0·49	−0·68
M. scalare	−5·08	−1·53	−1·37	−1·50
P. albimanus	−5·88	−1·06	−1·13	−1·45
P. ambiguus	−5·94	−1·25	−1·38	−1·84
P. angustatus	−5·21	−1·24	−1·15	−1·43
P. clypeatus	−4·87	−0·59	−0·61	−0·85
P. manicatus	−6·10	−0·79	−0·85	−1·16
P. peltatus	−5·56	−0·40	−0·44	−0·64
P. scutatus	−5·68	−1·21	−1·18	−1·32
P. tibialis	−4·84	0·11	0·07	−0·02
D. albostriatus	−5·63	0·39	0·26	0·06
E. eligans	−4·42	−0·40	−0·47	−0·77
E. balteatus	−4·84	0·08	0·06	−0·22
M. auricollis	−4·89	−0·76	−0·72	−0·94
M. corollae	−5·69	0·43	0·43	0·18
M. latifasciatus	−4·46	0·70	0·72	0·37
M. luniger	−5·18	0·43	0·45	0·16
S. scripta	−5·97	−1·82	−1·63	−1·73
S. ribesii	−4·88	0·60	0·58	0·16
S. vitripennis	−4·98	0·58	0·49	0·12
C. vernalis	−6·56	−0·06	−0·12	−0·41
R. campestris	−4·26	0·88	0·78	0·26
E. arbustorum	−5·65	0·48	0·01	−0·81
E. pertinax	−4·99	0·26	−0·35	−1·17
E. tenax	−5·86	0·45	0·09	−0·69
H. pendulus	−5·49	0·47	0·08	−0·69
E. strigatus	−5·04	0·19	0·15	−0·21
E. tuberculatus	−4·95	0·13	0·08	−0·22
M. equestris	−4·93	0·85	0·70	0·28
N. vitripennis	−5·54	0·36	0·42	0·05
P. noctiluca	−6·60	0·04	0·02	−0·34
S. pipiens	−5·44	−1·00	−1·35	−1·38