

## Ecomorphological relationships in hoverflies (Diptera, Syrphidae)

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Hoverflies spend most of their feeding time either taking nectar or pollen, in varying proportions according to species. *Xylota* species feed on pollen, but have a specialized method of collecting it from the surface of leaves.

Multivariate morphometric data and activity data (in the form of time-budgets) are associated by using canonical correlation analysis. The main feature of the two data sets lies in the correlation between proboscis shape and the proportion of time devoted to feeding on nectar and on pollen. Additionally, increased body size is correlated with more time feeding on nectar. The second canonical correlation documents the decrease in the proportion of time spent in flight with increasing body size.

Morphological similarity (distance apart in multivariate space) and ecological similarity (foraging niche overlap) are correlated. Species with similar size and shape feed on similar types of flowers and take similar foods (nectar or pollen).

Reproductive and energy requirements alter with body size, and these are sufficient to explain the observed differences.

### INTRODUCTION

The effects of body size upon ecological and behavioural characteristics of animals have been of interest to zoologists for a long time (Peters 1984). Western & Ssemakula (1982) argue that body size should constitute the primary cause of differences in life history parameters between species, against which other factors should be contrasted. Stearns (1983) investigated the influence of body size and phylogeny on patterns of covariation in mammalian life history traits; removal of the effects of body size left a significant but small effect of phylogeny.

Recently, interest has been shown in using morphology as an indicator of selective pressures on the niche (Ricklefs & Travis 1980). Thus it seems appropriate to consider not only the effects of body size but also those of shape upon ecological characteristics. A necessary part of such a research programme is to explore morphological patterns in relation to diet.

In a previous study of hoverflies, I concluded that dietary patterns for a small group of eight species of hoverfly could be related to mouthpart morphology

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(Gilbert 1981*a*). Elsewhere I have shown that the major axes of morphometric variability between species lie primarily in proboscis length relative to body size, and secondarily in aspects of body size uncorrelated with this (Gilbert 1985*a*). Building upon this, I use here the same morphometric data to test the hypothesis of adaptation to foraging behaviour, by using a multivariate technique. Once these features are established, community patterns of morphology can be analysed with greater confidence in their interpretation than would otherwise be possible (Gilbert *et al.* 1985).

#### MATERIALS AND METHODS

Hoverflies (Diptera, Syrphidae) are numerically important, often dominant visitors to many flower species. There are about 250 species in Britain (Stubbs & Falk 1983), mainly associated with woodland habitats (Speight *et al.* 1975). They are known to feed on both nectar and pollen (Müller 1883; Gilbert 1981*a*).

Three sites were surveyed weekly or fortnightly by using a standard census walk (Gilbert 1981*a*). The sites were the Cambridge Botanic Garden (BG), The Fellows' Garden of St John's College in Cambridge (FG), and Hayley Wood (HW), 18 km from Cambridge. BG and FG are both urban garden habitats, FG being more wooded and less manicured (see Gilbert 1981*a*), whereas HW is ancient deciduous woodland (see Rackham 1975). Each hoverfly seen was closely observed for a few seconds and identified: if feeding, its food was recorded as either pollen, nectar, or substances from leaf surfaces (which are principally pollen grains: see results). Summing observations over all dates and sites enabled the calculation of the percentage of the total number of a species seen carrying out the various categories of activity (resting, flying, feeding on pollen, feeding on nectar, gathering substances from leaf surfaces, or other). These data can be used as crude estimates of the time-budgets of individual flies. It is not known whether the proportions of time spent feeding on these foods can be equated with some measure of their relative importance in the diet, since ingestion rates are not known and may differ between species and foods.

By recording the type of flower visited and the food taken from it, I constructed a three-dimensional matrix of number of observations split into species  $\times$  flower type  $\times$  food. Converting these data into proportions of the totals for each species, I calculated overlaps in foraging behaviour by using the formula of Schoener (1970). The raw data for these calculations are available in Gilbert (1981*b*). These overlaps provide measures of similarity in foraging behaviour.

Morphometric data for 13 variables in total were collected from samples of hoverflies taken during the standard censuses (Gilbert 1985*a*). I converted these data to one size and six shape variables (Mosimann & James 1979), by defining log (head width) as a size variable (Gilbert 1985*b*) and subtracting it from the log-transformed data for five other variables (table 1). A sixth shape variable was formed from labellum length relative to prementum length (see Gilbert 1981*a*), a measure of the size of the food-gathering pads relative to the length of the proboscis.

Canonical correlation analysis (c.c.a.) relates a set of predictor variables to a set of response variables. The strategy is broadly analogous to principal components analysis, except that covariances between two sets of independent variables are used instead of variances to derive the new coordinate frame. The technique finds linear transforms of each set of variables such that the correlation between the transformed variables is maximized. The transformed variables are called canonical variates, and correspond to the axes of the new coordinate frame. There are  $s$  pairs of these linear transforms, where  $s$  is equal to the number of variables in the smaller of the two original sets, successive pairs of canonical variates after the first being uncorrelated with the preceding variate (see Gittins 1979). Here, c.c.a. is used to relate morphological variables of size and shape (predictor set) to a set of foraging variables (response set). These foraging variables consist of angular transformations of the percentages of observations in each category of activity. There are five categories (percentage pollen, percentage nectar, percentage flying, percentage resting and percentage feeding on any food). Since for each species, these must sum to 100% one variable (percentage resting) was omitted from the set to avoid circularity. Canonical correlation analysis was also run on all 13 original variables (log-transformed) as an interpretive check.

I included in the c.c.a. the technique of redundancy analysis (see Reyment 1976). This estimates the degree to which the variance of one set of variables is 'explained' by (redundant to) the variance of the other set, given the canonical correlation. Because of the symmetry of c.c.a. (there is no independent-dependent set, unlike regression), this redundancy can be considered in both senses, that is, the redundancy of set A given set B, and *vice versa*.

An estimate of morphological similarity between species can be obtained from 'statistical' distances (Mahalanobis'  $D^2$  values) between the centroids of species in the multivariate space generated by several multivariate statistical techniques. Values were taken from Gilbert (1985*a*), where the 13 original variables of the same data were used in a canonical variates analysis.

## RESULTS

### (a) Dietary patterns

Almost three times as many hoverflies were seen taking pollen as nectar (3275 and 1262, respectively), implying that the former is quantitatively the more important resource for the family as a whole. Wide variations occur between species (figure 1), from almost exclusively taking pollen (*Melanostoma* (M1 and M2 in figure 1), *E. balteatus* (S7), *S. ribesii* (S1)) to almost exclusively taking nectar (*R. campestris* (C2)). There is also a third pattern, of gathering material from leaf surfaces (*Xylota* (X1 and X2)). Dissection of the crops of these species demonstrates that they are collecting mainly pollen (Gilbert 1985*c*).

Females of most species were more often seen taking pollen than were males (Wilcoxon signed-rank test on percentages:  $T = 5$ ,  $P < 0.05$ ), and therefore each individual female probably spends more time feeding on pollen. This phenomenon is apparent in species from all parts of the nectar-pollen axis of figure 1.

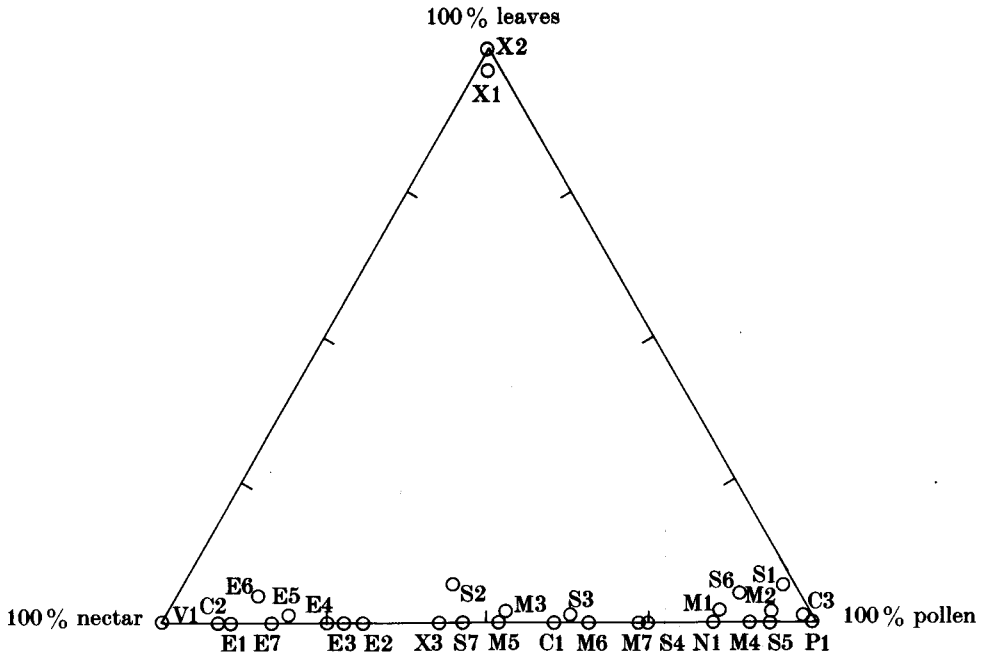


FIGURE 1. Feeding-time-budgets of hoverflies as estimated from standard census walks. The total number of individuals of each species was split into the proportions feeding on nectar from flowers, pollen from flowers, substances from leaf surfaces, and other foods. The triangular graph shows that most species feed from flowers, spending varying proportions of time feeding on nectar or pollen, depending on the species. Abbreviations of species are given in table 1.

(b) *Morphology and activity patterns*

Raw data are given in Table 1. Correlations within sets of variables (table 2) show that size is correlated with wing, thorax, and abdomen shape, but not with proboscis shape; within time-budget proportions, total feeding time is negatively correlated with flying time, positively with pollen feeding, but is uncorrelated with nectar feeding. Correlations between sets of variables (table 2) show that the proportion of time spent feeding on nectar and pollen are both strongly related to relative proboscis length and labellum shape.

Table 3 gives details of the eigenanalysis of the canonical correlation: only the first two roots are statistically significant, giving two significant canonical correlations. The components of these two sets of linear functions of the original variables (table 4) show that the first canonical factor represents the dominant trend of the data, the relationship between proboscis shape and the proportion of time spent feeding on nectar and on pollen (figure 2). Increasing proboscis length relative to body size is associated with an increasing proportion of time devoted to feeding on nectar, and a decreasing proportion to feeding on pollen. Labellum size relative to proboscis length is positively associated with increasing time spent feeding on pollen, and negatively with nectar feeding. Also associated with this trend is wing shape: those with relatively long wings tend to spend more time feeding on pollen, and less on nectar.

The second canonical factor represents the covariance between body size and the proportion of time spent flying, and is orthogonal to the first canonical factor: other variables (except proboscis shape) are associated with this factor by virtue of their correlation with size (table 2). Covarying with this body size–flying time relation is a nectar-feeding trend; increasing body size leads to relatively less time spent in flight, more time spent feeding, and in particular, feeding on nectar.

Total redundancy of the activity data, given the morphological data, is fairly high (table 4). Of this redundancy 66% is associated with the first canonical factor, and 21% with the second.

As a check, I ran c.c.a. again using all 13 log-transformed original variables, instead of converting to size and shape variables. In this case, there are again two significant roots. The first (canonical correlation, 0.98) reflects the relation between feeding on pollen ( $r = 0.96$ ), feeding on nectar ( $r = -0.77$ ) and proboscis length ( $r > 0.77$  for all four proboscis length-related variables). The second (canonical correlation, 0.93) is correlated with relative time spent flying ( $r = -0.43$ ) in the response set, and body size in the predictor set ( $r > 0.40$ ,  $P < 0.05$  for eight of nine variables not associated with proboscis length). Total redundancy (0.71) is higher, 56% associated with the first factor, 8% with the second. Both analyses pick out essentially the same features of the data.

### *(c) Morphology and feeding similarities*

Overlaps calculated here are indices of foraging similarities between hoverflies, measuring both the flowers they visit and the food they take (nectar or pollen). Mahalanobis'  $D^2$  values are measures of morphological similarity, actually distances apart in 13-dimensional space. Because the canonical variates analysis that generated these data (Gilbert 1985*a*) used covariances of log-transformed data, the morphological space described is undistorted with respect to the space described by the original variables. Figure 3 shows the relation between the two independent measures of similarity: they are correlated ( $r = -0.49$ ; d.f., 20;  $P < 0.01$ ). Thus, the more similar hoverflies are morphologically, the more similar are both the flowers they visit and the food that they take from those flowers.

The variance explained in this relationship is low ( $r^2 = 0.25$ ), probably partly because  $r$  is a linear degree of association, and the redundancy analysis for c.c.a. shows that some variables that contribute to statistical distances are not relevant to foraging.

## DISCUSSION

These results have demonstrated that the feeding behaviour of a group of animals is reflected in their morphology. Several factors could influence and determine the foraging patterns seen in figure 1. I consider two hypotheses, which are not mutually exclusive (Stearns 1983). These hypotheses are discussed assuming that observed differences in time-budgets reflect dietary differences. The fact that females are more often seen taking pollen provides support for this assumption. Hoverflies, despite the denial by Oldroyd (1964), feed extensively on pollen in the imaginal stage, as recognized by Müller (1883) and others (see Gilbert 1981*a*). In my earlier study (Gilbert 1981*a*), I suggested that the pseudotracheal

TABLE 1. CLASSIFICATION OF SPECIES MENTIONED IN THIS PAPER, ABBREVIATIONS USED ON THE FIGURES, AND DATA USED IN THE CANONICAL CORRELATION ANALYSIS

The response set is given here as proportions of the total number of individuals seen of each species for ease of study, but these are angular-transformed for c.e.a.

species	abbrevi- ation	size	w.l.	t.w.	t.l.	l.l.	t.2	t.3	pollen	nectar	flight	feed	N
Syrphinae													
Syrphini													
<i>Syrphus ribesii</i> L.	S1	0.5635	0.4502	-0.0907	-0.0257	0.1891	0.0598	0.0577	0.42	0.01	0.24	0.43	1333
<i>Metasyrphus corollae</i>	S2	0.4829	0.4362	-0.1249	0.0154	0.0813	0.0435	0.0435	0.37	0.40	0.04	0.77	845
<i>Scarena pyrastris</i>	S3	0.6425	0.4360	-0.1161	-0.0244	0.1919	0.0424	0.0442	0.46	0.27	0.08	0.73	26
<i>Leucozona lucorum</i>	S4	0.5416	0.4384	-0.1022	0.1504	-0.0084	0.0313	0.0393	0.13	0.04	0.33	0.17	24
<i>Meliscaena</i> spp.	S5	0.4281	0.5178	-0.0977	0.0080	0.1542	-0.0760	-0.0721	0.64	0.05	0.08	0.69	39
<i>Episyrphus balteatus</i>	S6	0.4843	0.5187	-0.0951	-0.0234	0.2007	0.0085	0.0057	0.57	0.06	0.20	0.63	2828
<i>Sphaerophoria scripta</i>	S7	0.3747	0.4335	-0.1546	0.1618	-0.0792	-0.1816	-0.1626	0.32	0.37	0.09	0.69	91
Melanostomatini													
<i>Melanostoma melinum</i>	M1	0.3139	0.4964	-0.1292	-0.0261	0.1293	-0.0490	-0.0490	0.42	0.04	0.22	0.46	300
<i>Melanostoma scalare</i>	M2	0.3464	0.5287	-0.1368	-0.0180	0.1399	-0.1532	-0.1368	0.44	0.03	0.30	0.47	912
<i>Platycheirus albimanus</i>	M3	0.3802	0.4643	-0.1322	0.1525	-0.0272	-0.1061	-0.1130	0.41	0.36	0.13	0.76	544
<i>Platycheirus clypeatus</i>	M4	0.3617	0.5040	-0.1442	-0.0374	0.1427	-0.0585	-0.0607	0.14	0.02	0.54	0.16	249
<i>Platycheirus manicatus</i>	M5	0.4425	0.4802	-0.1244	0.2468	-0.1543	-0.0789	-0.0845	0.12	0.11	0.68	0.23	266
<i>Platycheirus peltatus</i>	M6	0.4314	0.4890	-0.1112	0.1929	-0.0388	-0.0404	-0.0440	0.33	0.18	0.36	0.51	128
<i>Platycheirus scutatus</i>	M7	0.3385	0.4745	-0.1481	0.1284	0.0150	-0.1210	-0.1183	0.67	0.22	0.00	0.89	9
Eristalinae													
Pipizini													
<i>Pipiza austriaca</i>	P1	0.4065	0.4839	-0.0782	-0.1012	0.2341	0.0633	0.0544	0.73	0.00	0.06	0.73	33
Cheilosini													
<i>Cheilosia paganus</i>	C1	0.3345	0.4669	-0.0865	0.1017	0.0158	-0.0378	-0.0313	0.43	0.29	0.06	0.71	49
<i>Rhinga campestris</i>	C2	0.5051	0.4349	-0.0754	0.5173	-0.2304	0.0881	0.0780	0.08	0.69	0.12	0.77	26
<i>Ferdinandea cuprea</i>	C3	0.5211	0.4625	-0.0648	0.0598	0.1891	0.0315	0.0217	0.57	0.00	0.14	0.57	7

TABLE 1 (cont.)

species	abbrevi- ation	size	w.l.	t.w.	t.l.	l.l.	t.2	t.3	pollen	nectar	flight	feed	N
Chrysogasterini													
<i>Necoscia</i> spp.	N1	0.1492	0.4539	-0.1492	0.1295	0.0119	-0.2249	-0.0593	0.36	0.08	0.22	0.44	36
Volucellini													
<i>Volucella bombylans</i>	V1	0.6721	0.4272	-0.0636	0.2211	0.0542	0.1761	0.1636	0.00	0.47	0.00	0.47	19
Xylotini													
<i>Xylota segnis</i>	X1	0.4757	0.4568	-0.1083	-0.0624	0.2719	-0.1453	-0.1392	0.99	0.01	0.00	1.00	92
<i>Xylota sylvarum</i>	X2	0.5763	0.4506	-0.1230	-0.0605	0.3193	-0.1466	-0.1200	0.89	0.00	0.04	0.89	28
<i>Syrilla pipiens</i>	X3	0.3222	0.4427	-0.0969	0.2143	-0.0669	-0.0995	-0.1347	0.14	0.19	0.56	0.34	464
Eristalini													
<i>Helophilus pendulus</i>	E1	0.5786	0.3856	-0.0943	0.1695	-0.0198	0.0467	0.0079	0.06	0.48	0.02	0.54	52
<i>Eristalis arborescens</i>	E2	0.5899	0.3748	-0.0958	0.1449	-0.0200	0.0475	0.0011	0.27	0.60	0.02	0.87	252
<i>Eristalis intricarius</i>	E3	0.6848	0.3482	-0.0893	0.1425	-0.0274	0.0933	0.0467	0.07	0.20	0.44	0.27	41
<i>Eristalis nemorum</i>	E4	0.6170	0.3566	-0.0855	0.1662	-0.0356	0.0294	-0.0372	0.13	0.40	0.27	0.53	15
<i>Eristalis pertinax</i>	E5	0.6839	0.3920	-0.0996	0.1249	0.0576	0.0262	-0.0346	0.17	0.60	0.07	0.77	92
<i>Eristalis tenax</i>	E6	0.7226	0.3669	-0.0973	0.1667	-0.0536	0.0445	0.0090	0.15	0.68	0.01	0.84	336
<i>Myiatropa florea</i>	E7	0.6294	0.3859	-0.0659	0.1110	0.1219	0.0739	0.0228	0.08	0.34	0.01	0.42	79

Abbreviations: w.l., wing length; t.w., thorax width; t.l., proboscis length; l.l., labellum width; p.l., prementum length; h.w., head width; t.2, width of tergite 2; t.3, width of tergite 3.

TABLE 2. CORRELATION BETWEEN VARIABLES WITHIN AND BETWEEN PREDICTOR AND RESPONSE SETS

Only significant ( $P < 0.05$ ) correlations are given; where the correlation is highly significant ( $P < 0.001$ ), the figure is given in bold. Abbreviations as in table 1.

(a) Correlation matrix for size and shape variables

	1	2	3	4	5	6
1 log h.w.	1.00					
2 log w.l.—log h.w.	<b>-0.69</b>	1.00				
3 log t.w.—log h.w.	<b>0.59</b>	-0.38	1.00			
4 log t.l.—log h.w.	n.s.	-0.40	n.s.	1.00		
5 log l.l.—log p.l.	n.s.	0.37	n.s.	<b>-0.91</b>	1.00	
6 log t.2—log h.w.	<b>0.74</b>	-0.48	<b>0.78</b>	n.s.	n.s.	1.00
7 log t.3—log h.w.	0.56	n.s.	<b>0.68</b>	n.s.	n.s.	<b>0.91</b>

(b) Correlation matrix for activity data. Variables are angular transformations the proportion of individuals seen doing the various activities

	1	2	3
1 pollen	1.00		
2 nectar	<b>-0.61</b>	1.00	
3 flying	n.s.	n.s.	1.00
4 feeding	<b>0.63</b>	n.s.	<b>0.77</b>

(c) Correlations between morphological and activity data

	pollen	nectar	flying	feeding
1 log h.w.	n.s.	0.40	n.s.	n.s.
2 log w.l.—log h.w.	0.49	<b>0.65</b>	n.s.	n.s.
3 log t.w.—log h.w.	n.s.	n.s.	n.s.	n.s.
4 log t.l.—log h.w.	<b>0.66</b>	<b>0.68</b>	n.s.	n.s.
5 log l.l.—log p.l.	<b>0.68</b>	<b>-0.68</b>	n.s.	n.s.
6 log t.2—log h.w.	-0.52	0.38	n.s.	n.s.
7 log t.3—log h.w.	-0.46	n.s.	n.s.	n.s.

TABLE 3. EIGENANALYSIS FROM THE CANONICAL CORRELATION ANALYSIS

$\chi^2$  values are calculated by using  $\chi^2$  decomposition theory (Kullback 1959).

root	eigenvalue	percentage variance	canonical correlation	$\chi^2$	d.f.	$P$
1	0.8668	48.4	0.9310	149.7	10	below 0.001
2	0.5675	31.7	0.7534	30.2	8	below 0.05
3	0.2429	13.6	0.4929	7.4	6	n.s.
4	0.1155	6.4	0.3398	3.0	4	n.s.

canals of the labellum probably play an important role in pollen feeding, as well as their more conventional function in sucking up nectar and transporting saliva. This suggestion came from a correlation between pseudotracheal density and pollen feeding. Independently, Schuhmacher & Hoffmann (1982) have demonstrated that this is indeed the case.

All studies of adult nutrition and reproduction have confirmed that pollen feeding is vital for full egg maturation and oviposition (Schneider 1948; Doucette



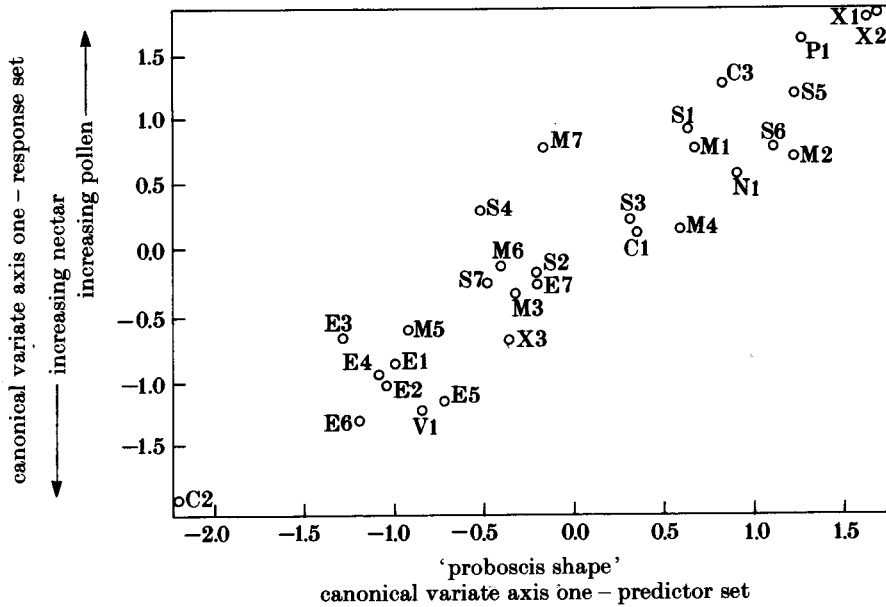


FIGURE 2. The first canonical factor in c.c.a. reflecting the relation between proboscis shape (length relative to body size, and labellum size relative to proboscis length) and feeding on nectar and pollen. This is the dominant relationship between the two sets of variables, accounting for 48% of the variance.

TABLE 4. DETAILS OF THE LINEAR FUNCTIONS OF THE ORIGINAL VARIABLES EXTRACTED IN THE FIRST TWO ROOTS

Loadings on the original variables are given, as well as the correlations of the original variables with the derived canonical variate. Only significant correlations ( $P < 0.05$ ) are given, with highly significant ones ( $P < 0.01$ ) in bold. Details of the redundancy are also given.

	first canonical variate		second canonical variate	
	loading	correlation	loading	correlation
predictor set				
log h.w.	-0.0345	-0.4187	-0.1590	<b>0.6206</b>
log w.l. - log h.w.	0.2033	<b>0.6665</b>	-0.3793	n.s.
log t.w. - log h.w.	0.3322	n.s.	-0.1310	0.6903
log t.l. - log h.w.	-0.3855	- <b>0.8559</b>	1.6102	n.s.
log l.l. - log p.l.	0.3757	<b>0.8659</b>	2.0164	0.3799
log t.2 - log h.w.	-0.8055	-0.4810	0.3081	<b>0.6267</b>
log t.3 - log h.w.	0.3288	n.s.	0.1886	<b>0.6602</b>
redundancy	0.3107		0.1579	
total redundancy	0.4988			
response set				
pollen	1.0691	<b>0.8575</b>	-3.3657	n.s.
nectar	-0.2254	- <b>0.8874</b>	-2.6575	n.s.
flight	-0.4155	n.s.	-0.5976	- <b>0.6442</b>
feeding	-0.7435	n.s.	2.4435	n.s.
redundancy	0.3396		0.0693	
total redundancy	0.4903			

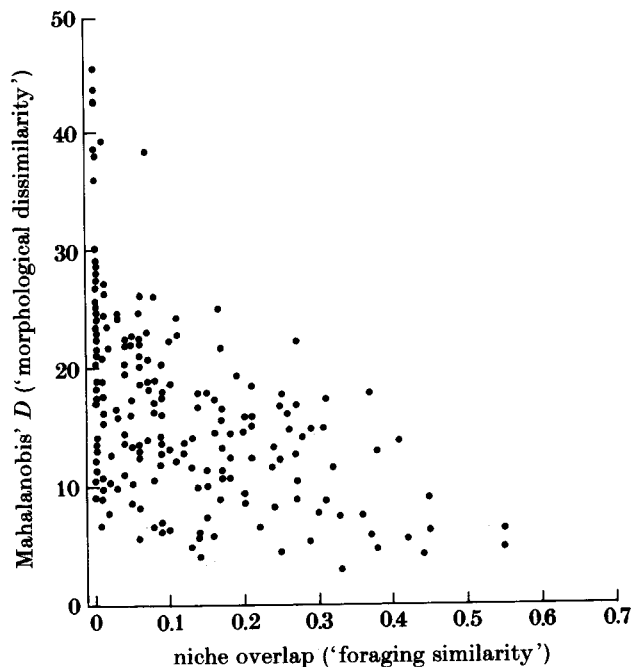


FIGURE 3. Relation between morphological and ecological similarity. Note that Mahalanobis'  $D^2$  values have been transformed by taking the square-root, and that this value gets larger as species are *less* similar morphologically. Dietary-overlap values get larger as species are *more* similar ecologically.

& Eide 1955; Stürken 1964; Adashkevich & Karelin 1972; Růžicka 1974; Maier 1978). Some eggs can occasionally be matured and laid without pollen feeding, but very low fecundities are thereby recorded (Cherian 1934; Lal & Lal Gupta 1953; Lal & Haque 1955; Doucette & Eide 1955; Tawfik *et al.* 1974; Awadallah *et al.* 1980; Ito & Iwao 1977). Different pollen species appear to differ in their effectiveness in promoting egg maturation and oviposition: Tanke (1976) found that *E. balteatus* rejected coniferous pollen; Kurir (1963) discovered that *Narcissus* pollen was an inadequate diet for both *Pipiza festiva* Mg. and *Heringia heringii* Zett.; and Saidov (in Way 1966) is reported to have found that the fecundity of *M. corollae* varies according to the type of pollen offered. The only quantitative study of the reproductive effects of pollen feeding was on *Mallota posticata* Fabr. (Maier 1978). Males may also require pollen to mature the reproductive tract (Kevan 1970; F. S. Gilbert, unpublished data; cf. Stoffolano 1974), but undoubtedly in much smaller quantities than females. Other foods are sometimes recorded (Curran 1924; Hunter 1896; personal observations), particularly honeydew (Lyon 1965).

Species might show differences in foraging because they are constrained by phylogeny; this hypothesis might state that the Syrphinae are predominantly adapted to feeding on pollen, whereas the Eristalinae are adapted to take varying proportions of nectar and pollen. A second hypothesis is that morphological factors (unrelated to phylogeny in the extreme version) might affect foraging behaviour.

Phylogenetic differences in foraging may arise because of differences in larval carry-over of nutrients into the adult stage (cf. Boggs 1981). Most Eristalinae larvae live in decomposing nutrient-rich organic matter of various kinds, the availability of which is probably more predictable than the evanescent aphid prey of the Syrphinae. Thus, aphidophagous species mature as quickly as possible, as there is every chance of their food supply vanishing, and starvation has drastic effects on adult fecundity (Růžička & Cairo 1976; Cornelius & Barlow 1980). They might leave most if not all reproductive nutrients to be collected during the adult stage. Since pollen contains protein and amino acids, and essentially nectar does not, adult female Syrphinae will feed on pollen. In the Eristalinae, however, the hypothesis suggest that a proportion of larval resources may be allocated to adult reproduction, and mostly energy is collected by adults.

This taxonomic hypothesis is falsified, however, by data from the genus *Platycheirus*, *P. clypeatus* (also *P. angustatus* Zett., *P. fulviventris* Macq. and *P. scambus* Staeg.: van der Goot & Grabandt (1970)) feeds exclusively on pollen, mainly from anemophilous flowers, whereas *P. albimanus*, *P. pellatus* and *P. manicatus* take increasing amounts of nectar.

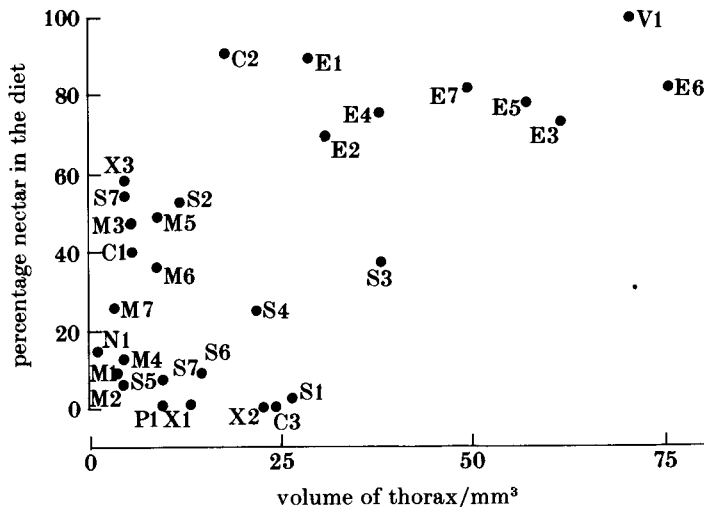


FIGURE 4. Relation between thoracic volume (cube of thoracic width) and the proportion of feeding time spent taking nectar. Note that species can be roughly divided into a group of pollen specialists (under 15% nectar), which are all small to medium-sized hoverflies, and a group where the percentage nectar increases with thoracic volume.

The second hypothesis provides an alternative explanation, and proposes that phylogenetic constraints are relatively unimportant, and that size and shape features determine foraging patterns. It emerges clearly from the results of the c.c.a., where the high redundancy associated with the first two canonical variates (table 4) is associated with proboscis shape and body size. Figure 4 shows explicitly the relation between the proportion of the total feeding time spent feeding on nectar and body size. Proportions can roughly be divided into virtually all pollen (under 15% nectar), and mixed (over 35% nectar); in the mixed-diet group,

percentage nectar increases with body size. We, therefore, have two phenomena: an increase of percentage nectar with body size, and the existence of pollen specialists.

Pollen specialization can be ascribed to the presence of starch and free sugars in pollen grains (Stanley & Linskens 1974, p. 129; Baker & Baker 1979). Instead of obtaining most of their energy from nectar, these species satisfy metabolic requirements with pollen. Since maximum crop volume increases linearly with body size (F. S. Gilbert, unpublished data), but energy requirements almost certainly increase in proportion to some fractional power of body size (Bartholomew 1981), the absence of large species feeding exclusively on pollen cannot be attributed purely to energetic considerations arising from body size. It must be postulated that much of the energy content of pollen is not readily available, but must be extracted by using enzymes: a process too slow for the activities of larger hoverflies. The strong negative relation between size and relative time spent in flight is suggestive that large species are under constraints to conserve energy. The greater energy requirements of mature males can also explain the switch from pollen feeding by immature males to nectar and honeydew by mature males (for example, in *S. ribesii*: Gilbert (1984)).

I reported elsewhere (Gilbert 1985a) that males of all species studied except *Xylota* have a relatively longer proboscis for their size. If males generally require more energy than females, and there is more energy (nectar sugar) in deeper corollae (Brink & de Wet 1980; Prÿs-Jones 1982), this is wholly consistent with the ecomorphological relationships reported here. The only exceptions prove the rule, for *Xylota* species do not visit flowers for food.

A similar hypothesis can explain the relation between nectar feeding and body size for the group with mixed diets (figure 4). Pollen may not release energy quickly enough for the absolute requirements of the larger species.

Thus the availability of energy in nectar and pollen, proboscis length relative to body size, and body size itself can account for the observed differences in patterns of foraging behaviour in hoverflies. Clearly, for small and medium-sized hoverflies, there are alternatives that can be adopted; perhaps phylogenetic inertia can be invoked here. Experimental tests are needed to substantiate the explanations offered here.

The approach of this paper is based on the premise that the morphologies of hoverflies should reflect their ecological relationships. It has demonstrated that morphological space can be closely mapped onto ecological space, and that accurate description, and hence predictions, of the time-budgets and hence probably the diets are possible by using rather few morphological measures. Tests of these predictions have been carried out (F. S. Gilbert, unpublished data). Ricklefs & Travis (1980) believe that morphological characteristics weight the varying selective pressures experienced during the seasons and throughout the life of an organism in proportion to the influence on fitness. The close parallels between morphology and foraging behaviour reported here indicate that such confidence may be justified, and, as claimed by Ricklefs & Travis (1980), that morphological analyses of communities constitute an independent measure of community structure with great potential for comparisons between habitats (see Gilbert *et al.* 1985;

James 1982; Travis & Ricklefs 1983). Phenetic packing can also be used as an indicator of community diversity (Findley 1973), and there would seem to be valuable lessons to be drawn from the integration of morphological and ecological methods. Both the type of flower visited, the food taken from the flower, and patterns of activity appear to be closely connected with morphology in syrphids. These results may help to integrate knowledge of plant-pollinator relationships when compared with those from other flower-visiting taxa.

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