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Morphometric patterns in hoverflies (Diptera, Syrphidae)

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Multivariate techniques are used to elucidate the main patterns of variation in morphology between and within species. The major difference between species lies in proboscis length relative to body size, and only secondarily in aspects of body size uncorrelated with this. Within species, sexual dimorphism is associated with differences in abdomen width, and variation between individuals of one sex is predominantly of size differences.

INTRODUCTION

Recently, increased interest has been shown in the use of morphological data to test ideas about the ecological characteristics of communities (Ricklefs & Travis 1980; James 1982). Most studies use only body size or some measure of mouthpart length to characterize 'morphology', although more sophisticated techniques are used in the description of relationships between bird communities and their habitats (James 1982). Few authors have attempted to discover quantitatively the major axes of variability between a group of related species, and then to relate these to morphology. Here I lay a morphological foundation for a study of ecomorphological relations among hoverflies (Gilbert 1985; Gilbert *et al.* 1985), by analysing variability in size and shape within and between species, allowing a quantitative exploration of the major differences.

I use multivariate morphometric techniques (Blackith & Reyment 1971), which have frequently been used in studies of insects; such studies are usually concerned with phylogeny or geographical variation (Gould & Johnston 1972), and include the only previous use of morphometric analysis in hoverflies (do Val 1972). Mosimann & Malley (1979) discuss several multivariate definitions of size and shape, and consider it important that two organisms that are geometrically similar with respect to a set of measurements should be recognized by a multivariate technique as having the same shape. The techniques used here do not allow such a recognition; however, in the present context I am not attempting to carry out rigorous statistical tests of differences in size and shape among species, but are merely identifying the major axes of variation within and between species, by using the methods in an exploratory role (Pielou 1977). For these purposes, the techniques used here are quite adequate (Blackith & Reyment 1971).

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Materials and methods

Hoverflies are very common visitors to flowers in the Holarctic. There are 250 species in Britain (Stubbs & Falk 1983). Species considered in this study are classified in table 1.

Samples of hoverflies were taken during a field study of foraging behaviour (Gilbert 1981*a*, 1985). Thirteen variables were measured on each specimen, chosen

Table 1. Classification of species of Syrphidae reported in this study, with species abbreviations as used in the figures

(Abbreviations identify tribal affiliation: nomenclature largely follows Stubbs & Falk (1983).)

subfamily	tribe	species	abbreviation
Syrphinae	Syrphini	*Syrphus ribesii* L.	S1
		S. vitripennis Mg.	S2
		Metasyrphus corollae Fabr.	S3
		Leucozona lucorum L.	S4
		Meliscaeva auricollis Mg & *cinctella* Zett.	S5
		Episyrphus balteatus deGeer	S6
	Bacchini	*Baccha obscuripennis* Mg.	B1
	Melanostomatini	*Melanostoma mellinum* L.	M1
		M. scalare Fabr.	M2
		Platycheirus albimanus Fabr.	M3
		P. clypeatus Mg.	M4
		P. manicatus Mg.	M5
		P. peltatus Mg.	M6
		P. scutatus Mg.	M7
Eristalini	Pipizini	*Pipiza austriaca* Mg.	P1
	Cheilosini	*Cheilosia paganus* Mg.	C1
		Rhingia campestris Mg.	C2
		Ferdinandea cuprea Scop.	C3
	Chrysogasterini	*Neoascia podagrica* Fabr.	N1
	Volucellini	*Volucella bombylans* L.	V1
		V. pellucens L.	V2
	Xylotini	*Xylota segnis* L.	X1
		X. sylvarum L.	X2
		Syritta pipiens L.	X3
	Eristalini	*Helophilus pendulus* L.	E1
		Eristalis arbustorum L.	E2
		E. intricarius L.	E3
		E. nemorum L.	E4
		E. pertinax Scop.	E5
		E. tenax L.	E6
		Myiatropa florea L.	E7

to reflect both size and shape (see table 2). From studies of bumblebees, it was expected that the proboscis might be important, and therefore five of the 13 variables concern the size of the parts of the proboscis as well as its overall length. Details of mouthpart structure are given in Gilbert (1981*a*). Rare species were not used in the morphometric analyses because of low sample sizes, but none are morphological outliers: full data are given in Gilbert (1981*b*).

I subjected these data to multivariate analyses. Canonical variates analysis (c.v.a.) (Campbell & Atchley 1981) was used to study variability between groups (species or sexes); principal components analysis (p.c.a.) (Blackith & Reyment 1971) described variation within groups. All variables were standardized to zero means and unit variances and $\log_{10}$-transformed.

Sample sizes were too small to assess adequately the degree to which these data conform to the assumptions of multivariate methods, namely the multinormal distribution and homogeneity of covariance matrices. It is very probable that they do not conform, as in most morphological data sets (Reyment 1971; Malmgren 1979). However, interpretation is limited to the major features, and I assume that the techniques are sufficiently robust to departures from the assumptions caused by these data (Crovello 1970; Reyment 1971; Malmgren 1979). I have confined interpretation in c.v.a. to the first two or three axes in the hope of avoiding other problems associated with this method (Campbell & Reyment 1978). Since I am using the techniques as data-exploratory methods rather than as hypotheses-testing procedures (Pielou 1977), minor departures from the assumptions can be tolerated since statistical tests are not the main aim.

Both c.v.a. and p.c.a. generate distances between groups or individuals in multivariate space: these can be calculated in various ways, and here I use the Mahalanobis' D^2 values produced by c.v.a. A minimum-spanning tree (Gower & Ross 1969) connects group means in c.v.a. that are closest together in multivariate space, and can be used to assess how accurately any pair of canonical axes (that is, two dimensions) reflect the true positions of the groups in multidimensional space.

Jolicoeur & Mosimann (1960) and Jolicoeur (1963) noted that the principal axes of p.c.a. were connected with size and shape factors. A unipolar axis, usually the first, reflects size, and subsequent bipolar axes measure the importance of shape factors. Recently it has been recognized that p.c.a. does not separate size from shape as efficiently as was thought (Mosimann & Malley 1979; Humphries *et al.* 1981), and here I identify as predominantly a size factor only a unipolar axis with coefficients of a similar magnitude.

Results

(*a*) *Interspecific comparisons*

Mean values for variables are shown in table 2; coefficients of variation vary between 5 and 20%. There is at least a 160-fold difference between the masses of the smallest and largest individuals in the study (male *Neoascia*, *Melanostoma*, *Baccha*, mass, 1 mg; female *Volucella pellucens*, mass, 164 mg), and other species elsewhere may range up to 300 mg (personal observation). This large range makes morphological and ecological comparisons particularly interesting.

The results of c.v.a. on species (table 3, column A) shows the first axis, containing the greatest proportion of between-group variance in relation to within-group variance, to be highly correlated with the four measures of proboscis length, but also positively correlated with all variables. The standarized canonical coefficients show, however, that this is a shape factor, with both positive and negative values.

TABLE 2. MEAN VALUES FOR THE 13 MORPHOLOGICAL VARIABLES FOR *N* INDIVIDUALS OF EACH SPECIES

(Sexes are separated for those species analysed for sexual dimorphism (see text). Abbreviations are: w.l., wing length; w.w., wing width; h.w., head width; t.w., thorax width; h.t., hind tibia length; t.l., proboscis length; f.l., fulcrum length; l.e., length of labrum-epipharynx; p.l., prementum length; l.l., labellum width; t.2, width of tergite 2; t.3, width of tergite 3; t.4, width of tergite 4.)

species	sex	w.l.	w.w.	h.w.	t.w.	h.t.	t.l.	f.l.	l.e.	p.l.	l.l.	t.2	t.3	t.4	*n*
S. ribesii	m	10.21	3.18	3.65	3.02	2.81	3.47	1.24	1.01	0.75	1.19	4.05	4.03	3.57	10
	f	10.44	3.19	3.67	2.91	2.72	3.43	1.24	0.96	0.80	1.18	4.36	4.34	4.03	10
S. vitripennis		9.59	2.99	3.43	2.70	2.49	2.98	1.13	0.89	0.73	1.09	3.92	3.91	3.91	8
Met. corollae	m	7.78	2.64	2.94	2.24	2.15	3.05	1.05	0.88	0.65	0.80	3.08	3.08	2.88	10
	f	8.76	3.14	3.14	2.31	2.32	3.25	1.11	0.93	0.70	0.85	3.61	3.62	3.43	11
L. lucorum		9.55	3.12	3.48	2.75	2.66	4.92	1.58	1.62	1.04	1.02	3.74	3.81	3.64	15
Meliscaeva		8.83	2.58	2.68	2.14	2.18	2.73	0.97	0.85	0.61	0.87	2.25	2.27	2.16	6
E. balteatus	m	9.80	2.88	3.06	2.56	2.42	2.89	1.04	0.84	0.64	1.05	2.88	2.88	2.67	10
	f	10.33	3.24	3.04	2.36	2.45	2.89	1.04	0.78	0.63	0.96	3.31	3.29	3.11	11
B. obscuripennis		7.28	1.98	1.72	1.11	1.64	1.64	0.63	0.43	0.35	0.54	0.41	0.90	1.26	8
M. mellinum	m	5.80	2.05	1.97	1.47	1.53	1.85	0.65	0.56	0.47	0.61	1.46	1.45	1.32	5
	f	7.00	2.42	2.13	1.58	1.67	2.01	0.70	0.61	0.51	0.71	2.16	2.17	2.12	6
M. scalare	m	7.59	2.44	2.32	1.72	1.76	2.12	0.75	0.67	0.50	0.67	1.25	1.31	1.28	10
	f	7.41	2.47	2.11	1.52	1.71	2.13	0.72	0.62	0.50	0.71	1.88	1.94	1.86	10
P. albimanus	m	7.09	2.16	2.44	1.84	1.73	3.52	1.12	1.02	0.67	0.63	1.63	1.59	1.47	10
	f	6.89	2.29	2.36	1.69	1.71	3.31	1.10	0.96	0.64	0.62	2.14	2.11	1.97	10
P. clypeatus	m	6.99	2.32	2.30	1.71	1.81	2.12	0.77	0.64	0.53	0.74	1.77	1.76	1.66	5
	f	7.53	2.52	2.31	1.62	1.83	2.11	0.76	0.63	0.54	0.76	2.14	2.12	2.01	9
P. manicatus	m	8.24	2.38	2.79	2.15	2.01	4.87	1.61	1.53	1.01	0.68	2.07	2.04	1.93	10
	f	8.50	2.77	2.74	2.02	1.97	4.91	1.54	1.47	0.93	0.69	2.55	2.51	2.31	10
P. peltatus	m	8.00	2.43	2.66	2.12	1.98	4.24	1.40	1.30	0.82	0.73	2.23	2.23	2.16	10
	f	8.42	2.74	2.74	2.06	2.05	4.17	1.41	1.26	0.82	0.78	2.69	2.65	2.51	10

P. scutatus		6.50	2.05	2.18	1.55	1.59	2.93	0.95	0.87	0.57	0.59	1.65	1.66	1.61	11
Pip. austriaca	m	7.44	2.61	2.45	2.15	2.03	1.95	0.63	0.55	0.47	0.82	2.79	2.71	2.45	7
	f	8.01	2.86	2.61	2.11	2.05	2.07	0.66	0.55	0.50	0.86	3.07	3.02	2.78	10
C. paganus	m	7.01	2.07	2.33	2.01	1.72	2.95	0.97	0.94	0.57	0.59	2.02	2.03	1.91	8
	f	5.78	1.94	2.03	1.57	1.50	2.56	0.84	0.81	0.51	0.55	1.95	1.99	1.88	10
R. campestris	m	8.47	2.66	3.15	2.70	2.25	10.78	2.90	2.79	2.02	1.19	3.73	3.62	3.19	10
	f	8.98	3.10	3.26	2.68	2.25	10.24	2.85	2.75	2.05	1.21	4.13	4.07	3.62	9
F. cuprea		9.63	2.97	3.32	2.86	2.52	3.81	1.18	1.20	0.77	1.19	3.57	3.49	2.94	5
N. podagrica		4.01	1.19	1.41	1.00	1.22	1.90	0.66	0.54	0.34	0.37	0.84	1.13	1.10	5
V. bombylans		12.57	4.47	4.70	4.06	3.92	7.82	2.45	2.42	1.58	1.79	7.05	6.85	5.55	7
V. pellucens		14.67	4.87	5.36	4.56	3.81	7.24	2.34	2.26	1.37	1.67	7.07	6.93	5.96	7
X. segnis	m	9.04	2.84	3.07	2.48	2.82	2.64	0.88	0.70	0.55	1.01	2.10	2.10	2.05	10
	f	8.09	2.65	2.91	2.18	2.54	2.53	0.86	0.66	0.53	1.01	2.17	2.25	2.21	10
X. sylvarum	m	11.53	3.44	3.95	3.11	3.55	3.45	1.17	0.89	0.70	1.54	2.77	2.85	2.69	3
	f	10.34	3.33	3.71	2.74	3.30	3.22	1.11	0.88	0.69	1.44	2.67	2.87	2.79	9
Syr. pipiens	m	5.48	1.80	2.01	1.59	1.89	3.35	1.04	0.96	0.67	0.57	1.50	1.25	1.34	10
	f	6.17	2.09	2.18	1.77	1.99	3.54	1.12	1.00	0.74	0.62	1.83	1.83	1.71	10
H. pendulus	m	8.95	2.93	3.73	3.04	3.06	5.52	1.73	1.75	1.11	1.07	4.15	3.72	3.05	9
	f	9.78	3.22	3.91	3.07	3.13	5.76	1.82	1.76	1.13	1.08	4.39	4.15	3.62	4
E. arbustorum	m	8.98	3.01	3.75	3.17	2.70	5.57	1.77	1.64	1.09	1.09	4.18	3.69	2.94	4
	f	9.30	3.19	3.94	3.09	2.82	5.38	1.70	1.62	1.11	1.05	4.40	3.98	3.34	11
E. intricarius		10.79	3.63	4.83	3.94	3.52	6.72	2.18	2.08	1.47	1.38	6.00	5.39	4.21	6
E. nemorum		9.41	2.96	4.14	3.40	3.06	6.07	1.96	1.92	1.27	1.17	4.43	3.80	3.17	6
E. pertinax	m	11.54	3.58	4.76	3.88	3.69	6.44	2.10	2.01	1.33	1.53	4.97	4.17	3.41	7
	f	12.27	3.93	4.91	3.80	3.69	6.44	2.08	1.96	1.35	1.53	5.28	4.75	3.98	7
E. tenax	m	11.55	3.82	4.97	4.05	3.68	7.52	2.34	2.30	1.52	1.25	5.44	4.87	3.93	6
	f	12.69	4.41	5.44	4.31	4.05	7.87	2.39	2.38	1.57	1.44	6.07	5.68	4.81	11
M. florea	m	10.40	3.44	4.21	3.74	3.40	5.54	1.78	1.68	1.09	1.44	5.00	4.41	3.34	10
	f	10.31	3.44	4.32	3.55	3.28	5.44	1.77	1.63	1.08	1.40	5.10	4.60	3.85	8

I interpret these as reflecting the covariance between proboscis length and body size. Thus, the main source of discrimination between species stems from differences in proboscis length relative to body size. Interestingly the fifth proboscis-related variable, labellum length, is not associated with this axis (table 3).

TABLE 3. RESULTS OF CANONICAL-VARIATES ANALYSIS OF THE MORPHOLOGICAL DATA, GIVING THE EIGENVALUES, STANDARDIZED CANONICAL COEFFICIENTS (S.C.C.), AND THE CORRELATIONS BETWEEN THE ORIGINAL VARIABLES AND THE DERIVED CANONICAL VARIATES (A, B, C)

(Only the first three canonical axes are given: others were not significant and represent little variance. Eigenvalues and correlations are given for three analyses: with sexes unseparated (A), with sexes separated (B), and with the outliers *Rhingia* and *Baccha* omitted (C). Only significant correlations are given ($P < 0.05$): those in bold type are highly significant ($P < 0.001$). Standardized canonical coefficients are given only for the analysis with sexes unseparated.)

	eigenvalues			percentage		
number	A	B	C	A	B	C
1	125.0	150.8	85.4	67.8	68.8	65.1
2	34.3	30.9	27.5	18.6	14.1	21.0
3	8.9	14.4	6.1	4.8	6.6	4.6

	canonical variate axes											
	one				two				three			
original variable	s.c.c.	A	B	C	s.c.c.	A	B	C	s.c.c.	A	B	C
w.t.	−0.08	0.37	n.s.	0.37	−0.06	**0.72**	**0.81**	**0.80**	−0.00	−0.37	n.s.	n.s.
w.l.	−0.50	n.s.	n.s.	n.s.	−0.49	**0.66**	**0.70**	**0.76**	0.03	−0.40	n.s.	n.s.
w.w.	0.12	n.s.	n.s.	n.s.	−0.15	**0.72**	**0.75**	**0.79**	0.14	n.s.	n.s.	n.s.
h.w.	−0.13	0.43	0.33	0.44	0.50	**0.77**	**0.83**	**0.83**	−0.12	n.s.	n.s.	n.s.
t.w.	−0.06	0.45	0.35	0.43	0.28	**0.79**	**0.85**	**0.84**	0.30	n.s.	n.s.	n.s.
h.t.	−0.28	n.s.	n.s.	n.s.	0.13	**0.77**	**0.85**	**0.86**	−0.45	−0.50	n.s.	n.s.
t.l.	0.29	**0.90**	**0.89**	**0.87**	−0.03	n.s.	n.s.	0.42	−0.02	n.s.	n.s.	n.s.
f.l.	0.39	**0.88**	**0.86**	**0.85**	−0.17	n.s.	0.41	0.45	−0.16	n.s.	n.s.	n.s.
l.e.	0.36	**0.91**	**0.90**	**0.90**	−0.11	n.s.	0.36	0.38	0.05	n.s.	n.s.	n.s.
p.l.	0.23	**0.87**	**0.86**	**0.82**	−0.10	n.s.	0.41	0.50	0.04	n.s.	n.s.	n.s.
l.l.	−0.23	n.s.	n.s.	n.s.	0.15	**0.76**	**0.82**	**0.90**	−0.18	−0.42	n.s.	n.s.
t.2	0.35	0.51	0.38	0.44	0.55	**0.81**	**0.84**	**0.83**	0.65	n.s.	n.s.	n.s.
t.3	−0.16	0.46	0.33	0.39	−0.05	**0.77**	**0.82**	**0.82**	−0.42	n.s.	0.36	n.s.
t.4	−0.02	0.41	0.29	n.s.	−0.15	**0.73**	**0.79**	**0.80**	−0.04	n.s.	0.38	n.s.

Normally the first canonical axis reflects mainly size differences (Blackith & Reyment 1971). Here, the second canonical axis discriminates on the basis of size variation that is independent of the covariance between proboscis length and size (table 3). Inspection of table 3 confirms that labellum length is highly correlated with this axis.

Group centroids along axes 1 and 2 are plotted in figure 1. Two things are apparent: first, that broad taxonomic groupings are more or less recognizable; and secondly that two species, *Rhingia campestris* (C2) and *Baccha obscuripennis* (B1), are sufficiently different from the others to qualify as outliers. *Rhingia* has by far the longest proboscis for its size of all European species, and *Baccha* has an aberrant long, petiolate abdomen. A minimum-spanning tree is drawn on figure 1, and it

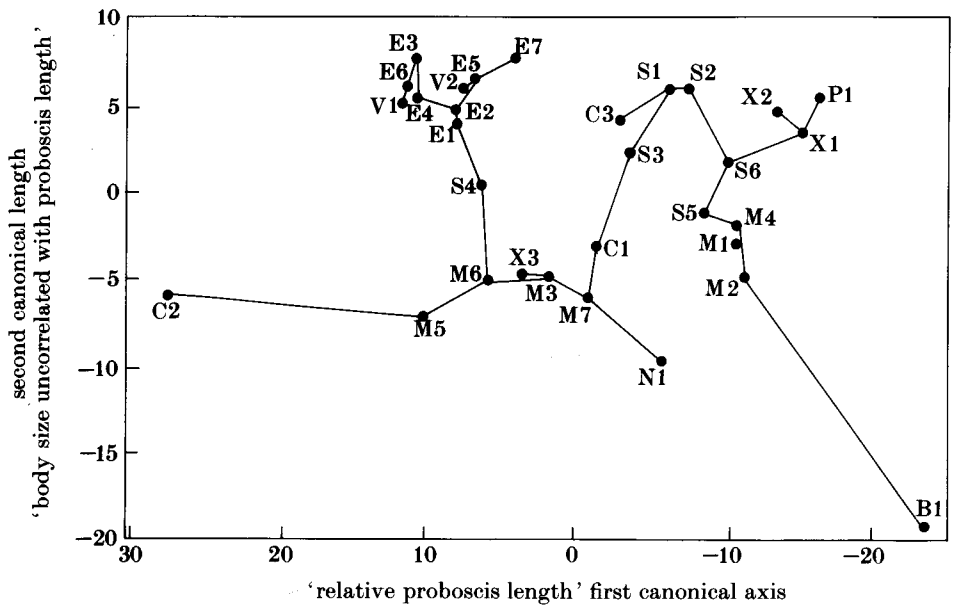

FIGURE 1. Canonical-variates analysis of 31 British hoverflies: plot of mean scores along the first two canonical axes. The first axis is correlated with proboscis length relative to body size, and the second with aspects of body size unrelated to the proboscis length–size covariance (see text). A minimum-spanning tree connects points closest together in multivariate space, and checks whether the two-dimensional graph accurately represents species positions in multivariate space. Species abbreviations as in table 2.

can be seen that these first two axes are fairly accurate at portraying the true multivariate (13-dimensional) separations. Assuming that the statistical assumptions are upheld by the data, all group centroids are significantly different from each other (F-test related to Hotelling's T^2, all are $P < 0.001$ except the two *Syrphus* species, where $P < 0.04$).

Outliers can bias the choice of axes (Campbell 1982), analogous with regression. The obvious candidates here are *Rhingia* and *Baccha*. The omission of these species merely disperses the groups in a smaller multivariate volume without altering their relative positions; standardized canonical coefficients are very similar for the first two axes, and the correlations between the axes and the original variables (table 3, column C) are almost identical.

(*b*) *Intraspecific comparisons*

Principal components analyses were performed on each species separately, for the 22 species with adequate sample sizes. An additional variable, mass, was included. In 21 cases, the first principal axis was unipolar with similar-sized coefficients, here interpreted as mainly reflecting a size factor. In the 22nd case, the contents of the crop caused independent mass variation sufficient to bias the choice of principal component 1. The first axis usually accounts for most of the variance (over 75 % in 19 cases). A typical data set (for *Cheilosia paganus*) is given

in table 4. The second axis usually (19 species) contrasts mass or thorax width with measures of abdomen width, and accounts for between 5 and 30 % of the variance. Mass varies independently of measures of abdomen width because of crop contents, egg development, and sexual differences in gonadal mass.

TABLE 4. RESULTS OF P.C.A. OF *CHEILOSIA PAGANUS*, GIVING THE EIGENVALUES AND EIGENVECTORS FOR SEXES LUMPED (A), MALES ONLY (M), AND FEMALES ONLY (F)

	eigenvalue			percentage of variance		
number	A	M	F	A	M	F
1	11.83	12.18	12.76	84.5	87.0	91.1
2	1.03	0.76	0.54	7.4	5.4	3.9
3	0.32	0.41	0.23	2.3	2.9	1.6
original	eigenvector 1			eigenvector 2		
variable	A	M	F	A	M	F
w.t.	−0.27	−0.26	−0.25	−0.04	0.09	0.50
w.l.	−0.27	−0.26	−0.28	0.26	0.30	0.03
w.w.	−0.28	−0.28	−0.27	−0.04	0.16	−0.13
h.w.	−0.26	−0.28	−0.24	0.14	0.13	−0.68
t.w.	−0.27	−0.28	−0.28	0.34	0.13	0.16
h.t.	−0.28	−0.26	−0.27	0.16	0.36	0.13
t.l.	−0.27	−0.25	−0.26	0.14	0.26	0.07
f.l.	−0.28	−0.28	−0.26	0.12	−0.05	0.37
l.e.	−0.27	−0.26	−0.27	0.19	0.06	−0.25
l.l.	−0.26	−0.23	−0.27	−0.25	−0.51	−0.03
t.2	−0.27	−0.28	−0.26	−0.29	−0.16	−0.04
t.3	−0.26	−0.27	−0.28	−0.44	−0.25	−0.08
t.4	−0.22	−0.24	−0.26	−0.59	−0.52	−0.14

(*c*) *Sexual dimorphism*

Mean vectors of each sex used in these analyses are given in table 2. In general females are larger than males, but some have larger males than females for all or some variables (*Cheilosia paganus*, *Melanostoma scalare*, *Myiatropa florea*, *Platycheirus albimanus* and *Xylota* spp.). Only in *C. paganus* and *Xylota* are males significantly heavier than females.

Canonical variates analysis of species with sexes as separate groups sheds light on the nature of sexual dimorphism. Correlations between canonical variates and the original variables (table 3, column B) show that the first canonical axis again contains covariance between proboscis length and body size, and the second contains size variation independent of canonical variate 1. These two axes poorly separate the sexes. The third canonical axis is best correlated with abdominal measures (table 3), and greatly increases the separation between sexes (figure 2). Group mean scores along canonical variate 1 (figure 2) demonstrate that in almost every case males have slightly higher positive scores than females (all save the two *Xylota* species: 18 of 20 species, binomial probability, 0.0001). This suggests that

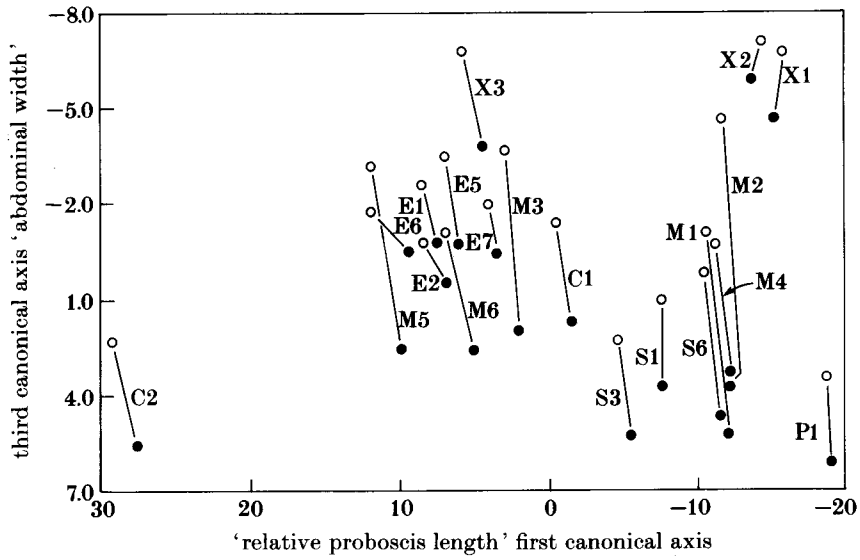

FIGURE 2. Canonical-variates analysis of 20 British hoverflies with data for the sexes separated: plot of the mean scores along the first and third canonical axes. The sexes of each species are connected with a line. Open circles denote males, closed circles denote females.

TABLE 5. DISTANCES APART IN MULTIVARIATE SPACE, AS MEASURED BY MAHALANOBIS' D^2, BETWEEN THE SEXES AND BETWEEN NEAREST-NEIGHBOURS (TO EITHER SEX)

(Figures obtained from a canonical variates analysis.)

species	distance apart (Mahalanobis' D^2) intersexual	nearest-neighbour
S. ribesii	12.8	40.8 (*E. balteatus*)
Met. corollae	21.4	47.9 (*S. ribesii*)
E. balteatus	43.9	40.8 (*S. ribesii*)
M. mellinum	66.0	11.0 (*P. clypeatus*)
M. scalare	108.0	11.8 (*P. clypeatus*)
P. albimanus	51.1	20.2 (*P. peltatus*)
P. clypeatus	29.1	11.0 (*M. mellinum*)
P. manicatus	53.2	37.5 (*P. peltatus*)
P. peltatus	27.2	20.2 (*P. albimanus*)
Pip. austriaca	15.7	104.9 (*M. mellinum*)
C. paganus	42.0	50.9 (*P. albimanus*)
R. campestris	26.3	395.9 (*P. manicatus*)
X. segnis	19.0	24.7 (*X. sylvarum*)
X. sylvarum	16.8	24.7 (*X. segnis*)
Syr. pipiens	49.2	83.2 (*P. peltatus*)
H. pendulus	14.2	17.0 (*E. arbustorum*)
E. arbustorum	14.0	17.0 (*H. pendulus*)
E. pertinax	17.5	33.1 (*H. pendulus*)
E. tenax	15.1	21.5 (*E. intricarius*)
M. florea	15.1	33.3 (*E. pertinax*)

the male has a relatively longer proboscis than the female, a significant factor in sexual differences in foraging (Gilbert 1975).

Mahalanobis' D^2 distances between the sexes can be used as a quantitative measure of sexual dimorphism, and can be compared with nearest-neighbour distances from either sex to other species (table 5). The Eristalini, *Metasyrphus corollae*, *S. ribesii* and *Xylota* have relatively small intersexual distances; *M. scalare* has the largest such distance. Nearest-neighbour differences bring out taxonomic relationships. There are three groups consisting of the Eristalini, Melanostomatini, and Syrphini, with the two *Xylota* species constituting a small separate group.

Principal components analysis of data for each sex suggests that nearly all variation among individuals of one sex is explicable purely by size differences. A typical result is shown in table 4. The first axis accounts for a very high proportion of the variance (over 87 % in *C. paganus*, table 4), although this may be an artefact of the low sample sizes.

Discussion

It has become biological dogma to state that organisms are adapted to their environment (Gould 1983), and that these adaptations are usually reflected in morphological features. I have described morphological diversification in British syrphids; the range of morphological space encompassed by the whole family is very wide, as can be seen from the diagrams of Hull (1949), Maki (1935) and Pino (1962). The earliest syrphids probably appeared more than 70 million years ago, and were possibly similar to the modern *Cheilosia* (Hull 1945, 1949; Röder 1980) or *Pipiza*. They probably were small, and had short mouthparts (see Röder 1980); it seems likely that pollen was their primary food source, if they fed from flowers. One can imagine relatively rare, random non-adaptive increases in size and changes in shape (Alberch *et al.* 1979), particularly in relative proboscis length. This may account for the distribution of proboscis length in syrphid species, since there are many more with a short, rather than a long proboscis (unpublished data).

Studies of bumblebees have often focused upon differences in proboscis length (Brian 1957; Henrich 1976; Inouye 1980), and there have been some excellent examinations of morphometric variability (Løken 1973; Pekkarinen 1979). None have attempted to define by quantitative multivariate methods what the important species differences are.

Among syrphid species, major differences between species appear to lie primarily in relative proboscis length, and only secondarily in aspects of body size unrelated to proboscis length. Labellar size also appears to be an important source of interspecific variation, its size being correlated not with proboscis size, but with body size independent of proboscis length. Intraspecific variability lies primarily in body size, particularly if the sexes are separated for analysis. Sexual dimorphism occurs to a greater or lesser extent in hoverflies, depending on the species involved, and is connected mainly with abdominal size and mass. Males consistently have a relatively longer proboscis than females, except in the two species (*Xylota*) that do not use their proboscis to collect food from flowers (Gilbert 1985).

Many treatments of inter- and intraspecific variation tacitly assume that the

shape of individuals does not alter with size, and use body mass as an index of size. However, size and shape are correlated intraspecifically even in species that vary little in mass (Mosimann & James 1979), and these differences in shape can often be related to ecological factors. Studies that measure only morphology and infer adaptation have been criticized (Gould & Lewontin 1979). In fact, several studies with both morphological and ecological data have concluded that there is no relationship between ecology and trophic morphology (Willson *et al.* 1975), and that observed morphological patterns are only in subtle ways different from the predictions of a random model (Ricklefs & Travis 1980). I have elsewhere described the diets of hoverflies (Gilbert 1981*a*), and related morphology to diet (Gilbert 1985) and to patterns of community structure (Gilbert *et al.* 1985).

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