

Size and shape variation in *Syrphus ribesii* L. (Diptera, Syrphidae)

BY F. S. GILBERT†

Department of Applied Biology, University of Cambridge,
Pembroke Street, Cambridge CB2 3DX, U.K.

(Communicated by Sir James Beament, F.R.S. – Received 28 September 1984)

Syrphus ribesii is a common and highly successful hoverfly. I identify here size and shape differences within and between the sexes. Males have shorter, relatively broader wings, a bigger thorax, and a narrower abdomen than females. The labellum, a fleshy pad at the end of the proboscis, is involved in feeding, and its size is closely correlated with body size in males, but varies more independently in females. Labellum size is the most important contributor to shape variance in females: abdomen size is the corresponding variable in males.

Male measurements show negative skewness and kurtosis both in individual variables and when compared with a multivariate-normal distribution. Females show no deviations from uni- or multivariate-normal distributions.

Adaptive reasons for these differences are suggested: male size and shape may be adjusted for the ability to catch females by high-speed chases in cool weather early in the morning; female shape may be influenced mainly by feeding behaviour.

INTRODUCTION

Within the 'adaptationist paradigm' (Gould 1983), it is assumed that differences in morphology and ecology between males and females of a species reflect the results of selective forces. Ecological effects of body size differences between species are well known (Western & Ssemakula 1982), and similar effects can occur within and between the sexes. For example, body temperatures in insects depend strongly upon size and shape (Digby 1955; Casey 1981), and thermoregulatory abilities can have important effects upon male mating behaviour (Gilbert 1984). Here, I use quantitative methods to describe and analyse differences in size and shape within and between the sexes of a common hoverfly, *Syrphus ribesii* L. This species was chosen because of my previous work with male mating behaviour (Gilbert 1984). Males and females are very similar, with only a subtle degree of sexual dimorphism (Gilbert 1985), but behaviourally they are very different.

† Present address: Department of Zoology, University of Nottingham, University Park, Nottingham NG7 2RD, U.K.

MATERIALS AND METHODS

Material for measurement was collected during field studies in Cambridge (U.K.) on hoverfly foraging (Gilbert 1981, 1985) and male mating behaviour (Gilbert 1984). Fourteen variables were measured on each of 105 male and 30 female flies (table 1).

Ordinary Discriminant Analysis (d.f.a.) is particularly useful for the study of sexual dimorphism, since it seeks a linear combination of variables that maximizes separation between two *a priori* groups. Overlap between groups can be evaluated statistically, and individuals positioned on the discriminant axis. Ordinary discriminant analysis assumes that covariance matrices are homogeneous, i.e. that the scatter of points in multivariate space has the same size and orientation in the two groups. Methods exist for analysing data with heterogeneous covariance matrices, and here I use one developed by Reyment (1969*a*), with additions and modifications by H. J. B. Birks. These modifications, include Dempster's analysis of covariance structure (see Reyment 1969*b*), and are implemented in a much-modified version of Blackith & Reyment's (1971) ORNTDIST program.

To analyse size and shape within each sex, principal components analysis (p.c.a.: see Blackith & Reyment 1971) was used. Jolicoeur & Mosimann (1960) noted that the principal axes of p.c.a. were connected with size and shape factors, the first axis usually containing most of the size variation between individuals. Recently it has been shown that these axes do not separate size and shape as efficiently as was thought (Mosimann & Malley 1979), and I identify as a size factor only an axis with loadings of a similar magnitude and sign.

All data were log-transformed to try to reduce problems of non-normality, although the effects of such a transformation can be erratic (Reyment 1971, 1973; Malmgren 1979). Nearly all multivariate statistical morphometric techniques assume that the data follow a multivariate-normal distribution: techniques differ in their robustness to departures from this assumption. I checked for the multivariate-normal distribution by using Mardia's method as described by Reyment (1971); this method requires very large sample sizes to stabilize the measures of skewness and kurtosis. The distribution of single variables was also assessed. All the multivariate techniques used covariance rather than correlation matrices.

RESULTS

Bivariate correlations between variables within a sex are all significant (all $P < 0.05$, 153 of 156 correlations have $P < 0.01$). Correlations are generally higher for females than the corresponding values for males in all cases except correlations with labellum length. In the latter instance, ten of twelve correlations are higher in males than females ($\chi^2 = 123.3$, 1 d.f., $P < 0.001$).

In univariate comparisons (table 1), the sexes are not significantly different for any measurement except thorax width (males larger than females) and the width of the abdominal tergites (females larger than males). Males are significantly less variable than females for every variable (variance-ratio of log-transformed data, Lewontin (1966), $F > 1.67$, $P < 0.05$).

TABLE 1. MORPHOLOGICAL DATA FOR THE SEXES OF *SYRPHUS RIBESII*, WITH TESTS OF SIGNIFICANT DIFFERENCES IN MEAN VALUES (*t* TEST) AND IN VARIABILITY (*F* RATIO TEST, FORMED FROM THE RATIO OF STANDARD DEVIATIONS OF LOG-TRANSFORMED DATA)

(* , $P < 0.05$; ** , $P < 0.01$; *** , $P < 0.001$. All measurements are in millimetres. For details of proboscis sclerites, see Gilbert (1981).)

variable	females ($n = 30$)		males ($n = 105$)		<i>t</i>	<i>F</i>
	mean	s.d.	mean	s.d.		
wing length	10.25	0.72	10.02	0.46	n.s.	2.42***
wing width	3.14	0.26	3.14	0.18	n.s.	2.14**
head width	3.55	0.26	3.60	0.16	n.s.	2.81***
thorax width	2.82	0.23	3.05	0.15	**	2.69***
tibia length	2.66	0.19	2.79	0.14	n.s.	2.05**
proboscis length	3.33	0.32	3.41	0.24	n.s.	1.75*
fulcrum length	1.20	0.11	1.21	0.06	n.s.	2.77***
labrum-epipharynx	0.96	0.09	1.00	0.07	n.s.	1.92**
prementum length	0.78	0.06	0.78	0.04	n.s.	2.13**
labellum length	1.24	0.12	1.28	0.09	n.s.	2.10**
tergite 2 width	4.21	0.37	3.97	0.24	*	2.17**
tergite 3 width	4.17	0.36	3.92	0.24	*	2.09**
tergite 4 width	3.87	0.36	3.50	0.25	***	1.67*

The results of the ORNTDIST analysis show that the sexes are amply distinct with 100% correct classification of individuals, that is, no overlap along the discriminant axis of any method. The main discriminating variables are the wing length, thorax width, and the width of the abdominal tergites (table 2*b*). Females have longer and relatively narrower wings, but smaller thoraces: the fourth abdominal segment is much wider in females than males.

We can regard the scatter clouds of observations, represented in terms of the covariances (table 2*a*), as ellipsoids. ORNTDIST reveals that these ellipsoids of scatter in multivariate space have significantly different degrees of inflation (comparing covariances by an *F*-test, $P \ll 0.001$ in many cases), and their relative orientations are significantly different (table 2*c*). A test for homogeneity of covariance matrices based on Kullback's (1959) β -distribution gave $B^2 = 163.83$ for $\beta^2 = 14.90$ and 91 degrees of freedom ($P \ll 0.001$). This heterogeneity of orientation implies differences in the growth patterns between males and females. Despite the heterogeneity, the various methods of calculating the 'statistical distance' between the sexes do not produce very different results (table 2*b*). Dempster's analysis of covariance structure demonstrates the same phenomenon. As Reyment (1969*b*) explains, *k* values indicate whether the orientations of the two ellipsoids of scatter of the data are the same, or at different angles. The expected value for all three *k* values is 1.00. Here, clearly the orientations of the ellipsoids are different. Reyment's own method of assessing similarity in orientation (table 2*c*) gives the same result: at least all the first five axes are not collinear.

Patterns of variations within each sex are shown by p.c.a. (table 3). The first component is mainly one of size in both sexes explaining more of the variance in females (81.5%) than males (67.9%), although some shape covariance is also

(b) discriminant function

variable	coefficients of the discriminant function†			
	A	B	C	D
wing length	223.8	339.1	308.3	484.8
wing width	28.4	-14.1	-5.0	-50.1
head width	-18.7	-1.5	-2.4	-11.2
thorax width	-221.3	-221.9	-221.0	-221.0
hind tibia	-98.0	-116.9	-109.5	-165.0
proboscis	16.4	-6.5	-2.0	-21.1
fulcrum	-6.4	5.4	2.2	21.7
labrum-epipharynx	-66.6	-87.3	-81.5	-113.6
prementum	27.7	5.3	11.3	-22.8
labellum	5.9	6.6	5.9	8.8
tergite 2	123.9	110.7	111.3	122.7
tergite 3	-132.3	-152.5	-144.9	-202.6
tergite 4	123.9	160.9	150.8	208.2
'statistical' distance	16.8	18.8	18.5	22.6

† Discriminant functions calculated with different methods: A, Standard method with Mahalanobis's generalized distance. Hotelings $T^2 = 391.7$, $F_{13, 121} = 27.41^{***}$; B, Anderson and Bahadur's method for heterogeneous matrices; C, method for heterogeneous matrices based on averaging covariance matrices; D, Dempster's method with D -delta, $k = 1.22$, $k_1 = 1.03$, $k_2 = 1.71$.

(c) orientation of ellipsoids

vector	χ^2	d.f.	P
1	33.29	12	0.001
2	35.75	12	0.0004
3	55.85	12	0.0
4	28.34	12	0.005
5	31.11	12	0.002

data some variables show negative skew ($P < 0.001$) and positive and negative kurtosis ($P < 0.001$). Tests for multivariate-normality are tentative, especially for females, because of relatively low sample sizes. However, similar patterns are evident. Data for females have a suspiciously close agreement with the multivariate-normal distribution ($\beta_{1, 13} = 77.7$, $\chi_{455}^2 = 388.7$, $P = 0.99$), the implications of which are not clear. Data for males show significant skewness ($\beta_{1, 13} = 63.4$, $\chi_{455}^2 = 1110.1$, $P = 0.0$) and kurtosis ($\beta_{2, 13} = 243.5$, $P < 0.05$).

DISCUSSION

Sexual dimorphism has been noted in a great many animals, but has less commonly been quantified by using multivariate methods, despite the obvious multivariate nature of the problem. Reyment (1969*a*) discusses in detail the sexual dimorphism of various animals, and finds that in many cases the dispersion ellipsoids of males and females are significantly differently inflated, and their major axes significantly differently oriented, as found here. As in some of Reyment's examples, the mean values of the variables for the sexes of *S. ribesii* are very close, but the inflation and orientation of the scatter ellipsoids are very different. This

TABLE 3. PRINCIPAL COMPONENTS ANALYSIS OF THE SEXES OF *S. RIBESII*: EIGENVALUES, AND CORRELATIONS BETWEEN ORIGINAL VARIABLES AND THE PRINCIPAL COMPONENTS

(Only axes that contain more than 5% of the variation are shown. Only significant correlations are given. Abbreviations of variable names as in table 2.)

	principal components				
	one		two		three
	male	female	male	female	male
eigenvalue	0.00601	0.01484	0.00130	0.00146	0.00054
percentage variance	63.2	81.5	13.7	8.0	5.7
original variable					
w.l.	0.84	0.96	n.s.	n.s.	n.s.
w.w.	0.88	0.91	n.s.	n.s.	0.26
h.w.	0.94	0.97	n.s.	n.s.	n.s.
t.w.	0.87	0.95	n.s.	n.s.	n.s.
h.t.	0.87	0.95	n.s.	n.s.	n.s.
t.l.	0.75	0.85	-0.30	n.s.	-0.56
f.l.	0.88	0.95	n.s.	n.s.	n.s.
l.e.	0.80	0.94	-0.27	n.s.	0.27
p.l.	0.83	0.94	-0.22	n.s.	n.s.
l.l.	0.74	0.61	-0.38	-0.77	n.s.
t.2	0.85	0.94	0.47	n.s.	n.s.
t.3	0.84	0.94	0.49	n.s.	n.s.
t.4	0.79	0.92	0.52	n.s.	n.s.

implies only moderate sexual dimorphism in size, but strong sexual dimorphism in growth pattern. Among other syrphids, some show strong dimorphism in size (for example, *Cheilosia variabilis*) or shape (for example, *Sphaerophoria scripta*) (F. S. Gilbert, unpublished data).

Do Val (1972) found almost exactly the opposite trend in the morphology of the three South American *Ornidia* species that he measured. The males had longer and narrower wings than the females, while the latter generally had broader thoraces. This is puzzling, for in all species I have looked at (Gilbert 1985), the trends are similar to *S. ribesii*. Bivariate regression of wing length (x) against wing width (y) for individuals of all species reported in Gilbert (1985) shows that the slopes of the major axis are significantly different between the sexes (slopes $\pm 95\%$ confidence limits: females, slope = 2.91 ± 0.10 ; males, slope = 3.10 ± 0.11). Male wings are in all species shorter and broader than the wings of females. Aerodynamically hoverflies are particularly interesting (Ellington 1984). It is well known that shorter, broader wings are associated with greater manoeuvrability, and male mating behaviour (Gilbert 1984) provides the rationale for believing that wing shape is adaptive.

I have shown elsewhere that thermoregulation appears to be an important feature of male biology in *S. ribesii*, and may perhaps be related directly to mating success (Gilbert 1984). It is, therefore, interesting that males have larger thoraces, which will retain heat better. Populations in Scotland have relatively larger

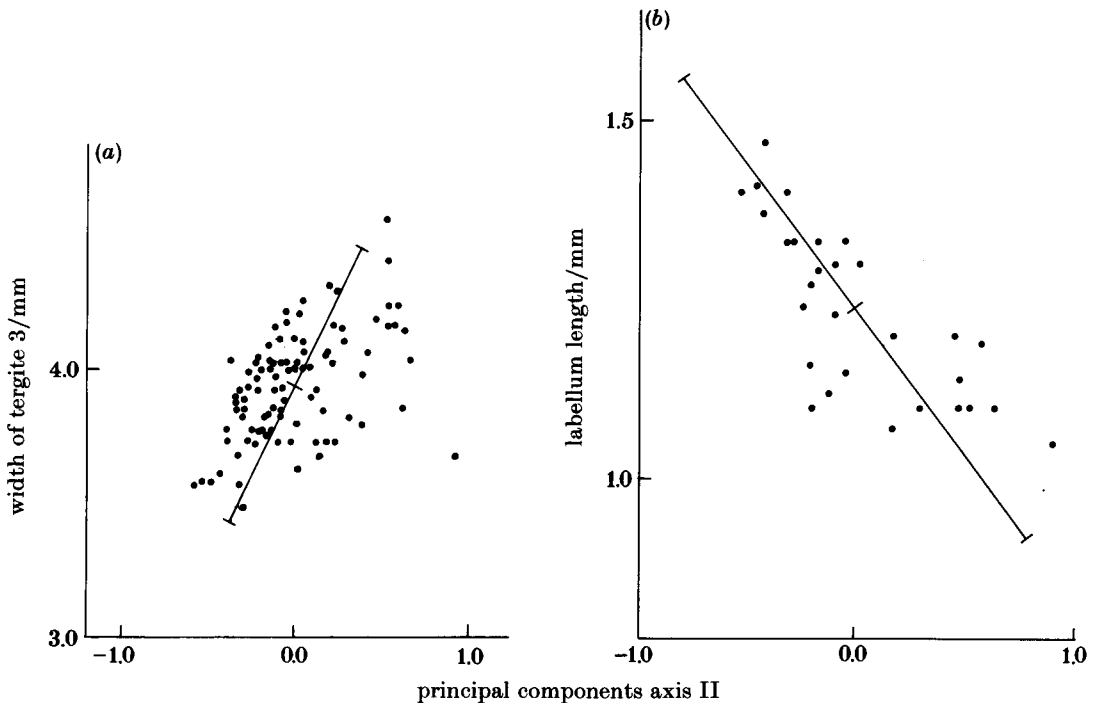


FIGURE 1. Plot of scores along p.c.a. II against the original variable most highly correlated with these scores. For males (a) this variable is the width of the abdomen; for females (b), it is the length of the labellum.

thoraces than southern populations of *S. ribesii* (F. S. Gilbert & G. E. Rotheray, unpublished data). Males may also use their abdomens as heat collectors or dissipators (cf. *Bombus*: Heinrich 1979), and the main shape factor appears to be an allometric change in abdomen size.

Differences in the distribution of variables are of some interest. Brown (1979) has noted that skewness and kurtosis may be an inherent property of wild populations, since selection may act disproportionately against very small individuals. If this is the source of non-normality, then selection appears to act strongly in males, and to be weak or absent in females. If the ability to thermoregulate is directly related to mating success, this could constitute a powerful selective force against small males: small male *S. ribesii* lose heat twice as rapidly as large ones (Gilbert 1984).

I thank S. A. Corbet, P. G. Willmer, O. E. Prŷs-Jones, D. M. Unwin, and especially H. J. B. Birks for help with this work. I was supported by a Natural Environment Research Council Studentship during the field work, and by the Commonwealth Fund of New York and Gonville and Caius College during writing.

REFERENCES

- Blackith, R. E. & Reyment, R. A. 1971 *Multivariate morphometrics*. London: Academic Press.
- Brown, K. R. 1979 Comparative wing morphometrics of some acalyptrate Diptera. *J. Austr. ent. Soc.* **18**, 289–303.
- Casey, T. M. 1981 Behavioral mechanisms of thermoregulation. In *Insect thermoregulation* (ed. B. Heinrich), pp. 79–114. New York: Wiley.
- Digby, P. S. B. 1955 Factors affecting the temperature excess of insects in sunshine. *J. exp. Biol.* **32**, 279–298.
- Ellington, C. P. 1984 The aerodynamics of hovering insect flight. *Phil. Trans. R. Soc. Lond. B* **305**, 1–181.
- Gilbert, F. S. 1981 Foraging ecology of hoverflies (Diptera, Syrphidae): morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecol. Ent.* **6**, 245–262.
- Gilbert, F. S. 1984 Thermoregulation and the structure of swarms in *Syrphus ribesii* L. (Syrphidae). *Oikos* **42**, 249–255.
- Gilbert, F. S. 1985 Morphometric patterns in hoverflies (Diptera, Syrphidae). *Proc. R. Soc. Lond. B* **224**, 79–90.
- Gould, S. J. 1983 The hardening of the modern synthesis. In *Dimensions of Darwinism* (ed. M. Grene), pp. 71–93. Cambridge: University Press.
- Heinrich, B. 1979 *Bumblebee economics*. Cambridge, Massachusetts: Harvard University Press.
- Jolicœur, P. & Mosimann, J. E. 1960 Size and shape variation in the painted turtle: a principal component analysis. *Growth* **24**, 339–354.
- Kullback, S. 1959 *Information theory and statistics*. New York: Wiley. 395 pages.
- Lewontin, R. C. 1966 On the measurement of relative variability. *Syst. Zool.* **15**, 141–142.
- Malmgren, B. A. 1979 Multivariate normality tests of planktonic foraminiferal data. *Math. Geol.* **11**, 285–297.
- Mosimann, J. E. & Malley, J. D. 1979 Size and shape variables. In *Multivariate methods in ecological work* (ed. L. Orloci, C. R. Rao & W. M. Stiteler), pp. 175–189. Maryland: Int. Co-op. Publ. House.
- Reyment, R. A. 1969a Some case studies of the statistical analysis of sexual dimorphism. *Bull. geol. Inst. Univ. Uppsala* NS **1**, 97–119.
- Reyment, R. A. 1969b Covariance structure and morphometric analysis – a contribution to paleogenetics. *Math. Geol.* **1**, 185–197.
- Reyment, R. A. 1971 Multivariate normality in morphometric analysis. *Math. Geol.* **3**, 357–368.
- Reyment, R. A. 1973 The discriminant function in systematic biology. In *Discriminant analysis and applications* (ed T. Cacoullos), pp. 311–337. London: Academic Press.
- do Val, F. C. 1972 On the biometry and evolution of the genus *Ornidia* (Diptera, Syrphidae). *Papeis Dep. Zool., São Paulo* **26**, 1–28.
- Western, D. W. & Ssemakula, J. 1982 Life-history patterns in birds and mammals and their evolutionary interpretation. *Oecol., Berl.* **54**, 281–290.