

## Morphological approaches to community structure in hoverflies (Diptera, Syrphidae)

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Simulation techniques are used to generate random communities of hoverflies that can be compared with observed communities: both the species composition and morphological size ratios are compared. Patterns of morphology are also examined through the study of size ratios within taxa.

Three sites were surveyed, two man-made garden habitats, and one ancient woodland. The man-made habitats contained assemblages of species indistinguishable from species assembled randomly from those present in the county (area = 3400 km<sup>2</sup>) as a whole, given the assumptions of the random model. The ancient woodland site contained significantly fewer species in common with the man-made habitats than expected from the random model.

Size ratios (of both absolute and relative proboscis length) show a similar pattern, with non-random (constant) ratios observed among the common species in ancient woodland.

Significantly constant proboscis length ratios were detected in two genera, *Eristalis* and *Platycheirus*. In the former, these are due to regular ratios of general body size. In *Platycheirus*, species have significantly regular differences in relative as well as absolute proboscis length.

### INTRODUCTION

Morphological approaches to interspecific relationships have been fashionable for some time (Hespenheide 1973; Karr & James 1975). Detailed analysis of single sites over several years may reveal decidedly complex patterning (Wiens & Rotenberry 1980) that can lead to a denial that any detectable community structure pertains in these systems (Wiens & Rotenberry 1981). One source of evidence marshalled to support the existence of competitively based structuring of communities is a

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regular spacing of morphological parameters, particularly the body mass or dimensions of mouthparts (Hutchinson 1959; Bowers & Brown 1982), and this has been codified as a 'constant' (Maiorana 1978). Løvtrup (1977) and Løvtrup *et al.* (1974) tried to show that regular body size differences constitute evidence for the punctuated equilibrium model of evolution. However, the evidence for the existence of size ratios has been intensively discussed in recent years (Simberloff & Boecklen 1981; Roth 1979, 1981; Wiens 1982, 1983).

Flower foragers form a distinct feeding guild, obtaining all or most of their nutrients from pollen or nectar. There is no *a priori* reason why competition for nectar should be 'severe', as envisaged by Brown *et al.* (1978). Competition for nectar is a reasonably well established phenomenon among hummingbirds, since resource limitation has been suggested (Montgomerie & Gass 1981), and territorial behaviour is known to be correlated with (Gill & Wolf 1975) and caused by energetic considerations (Carpenter & MacMillen 1976; Ewald 1980). The two prerequisites for competitive structuring of communities, resource limitation and competition, have also been demonstrated in bumblebees (Heinrich 1976; Inouye 1978*a*), and the effects are known of proboscis and corolla tube lengths on the patterns and rates of visitation (Inouye 1980). However, even bumblebee communities may show little evidence of spacing of proboscis lengths (Ranta & Lundberg 1980), and thus several *ad hoc* hypotheses may be needed to preserve the paradigm of competitively determined community structure (Ranta & Vepsäläinen 1981).

Here we analyse communities of hoverflies visiting flowers at three sites in or near Cambridge, England. Bees, mainly *Bombus* and *Apis*, formed less than 20% of foragers at flowers, and were usually found on flowers not used by syrphids. Hoverflies were overwhelmingly dominant numerically, and, therefore, interacted mainly with each other. For the morphometric analyses, we chose to consider the 35 commonest species overall (forming 98.5% of all individuals), and the 10 commonest in each site (constituting 78%, 84%, and 94% of syrphid visitors to flowers in the three sites).

We use three methods of assessing community structure. The first is the calculation of dietary overlaps for a comparison between sites that differ in the number of resource types that they offer. For many, if not most species, the use of overlaps to discover a 'limiting similarity' cannot now be seriously regarded as revealing any fundamental attribute of species interactions (Abrams 1976; Wiens 1977), but their calculation can be useful for assessing dietary similarities. For a few organisms, overlap may indicate interaction (Högstedt 1980; Pacala & Roughgarden 1982).

The second method uses a modified simulation technique (Connor & Simberloff 1978) that has been useful in testing the composition of communities (Simberloff 1983). The use of some models that use the null hypothesis of random assignments of species into 'communities' has been criticized (Diamond & Gilpin 1982; Harvey *et al.* 1983; but see Connor & Simberloff 1983). It is important to explore the limits of these models to examine their usefulness to ecological problems (see Strong 1980).

Finally, we analyse communities from a morphological standpoint. To accomplish this with any degree of confidence, a chain of questions must be answered. One

must discover those variables that contribute most to interspecific variability in morphology, and it must be established that these bear a strong relationship to differences in the ecology of the species in the community. Only then are we justified in using the identified major components of variability as indicators of ecological relationships in analyses of community structure (Ricklefs & Travis 1980). One of us has shown elsewhere (Gilbert 1985*a, b*), first by canonical variates analysis and secondly by canonical correlation, that the major morphological difference between hoverfly species lies in the length of the proboscis relative to body size, and that relative proboscis length is closely correlated with dietary differences. We therefore feel justified in using the absolute and relative proboscis lengths in the morphological analyses presented here, the latter being represented by the mean scores of the species along the first canonical axis (which represents proboscis length relative to body size: see Gilbert 1985*a*). Coefficients of variation of both measures are low (under 10%).

In view of the controversy surrounding the use of null models in community ecology, it is perhaps useful to state explicitly the sequence of tests reported in this paper. First, we analyse the three syrphid communities by using a colonization model, to test whether the species composition can reasonably be regarded as a random sample of all species that occur in the county. In the random colonizing of the species (rows) by sites (columns) matrix, only column totals are held constant. If the composition is non-random, then we ask whether this is due to competition acting through morphology. This is accomplished by testing whether there are constant or minimum size ratios. If size ratios are not distinguishable from random expectation, we interpret non-random species composition in terms of habitat selection or competitive exclusion mediated by some other mechanism. If size ratios are more constant than random expectation, then we expect to see some minimum ratio if competitive exclusion is mediated by proboscis length differences. As a separate question, we ask whether evolutionary forces have caused proboscis length ratios of all syrphids that could potentially compete to be different from random expectation.

#### MATERIALS AND METHODS

Hoverflies form one of the commonest of flower-visiting groups, and are often numerically dominant in many forager communities, particularly at high latitudes (Chernov 1966; Hippa *et al.* 1981). With more than 5300 species known, they are also one of the more diverse of dipteran families. Although important pollinators, they are often omitted from studies of floral biology. The British fauna contains about 250 species (Stubbs & Falk 1983), and is without doubt one of the best known of any region. Most syrphids are associated with woodland habitats of one type or another. Table 1 gives a classification of species mentioned in this paper.

Data on flower visiting patterns were obtained from standard census walks (see Gilbert 1981) carried out weekly or fortnightly during 1979 (two urban sites) and 1980 (an ancient woodland site). The urban sites were the Botanic Garden of Cambridge University (BG: a site with 183 visited flower species), and the Fellows' Garden of St John's College, Cambridge (FG: 67 visited flower species that bloom

mainly in the spring). Hayley Wood (HW: 32 visited flower species) is an ancient boulder-clay wood (Rackham 1975), with mainly spring flowers. Each flower was considered to provide two distinct resources, nectar and pollen, with visits for each recorded separately. The matrices of visits to resource types by hoverfly species, converted to frequencies, were used in the standard manner to calculate dietary overlaps, by using the formula of Schoener (1970). Overlaps were subjected to cluster analysis (see Aho *et al.* 1981), using a minimum-variance clustering criterion ('optimal sum-of-squares', Orloci 1967). Sites differed greatly in the number of visited flowers (always more or less all the available flowers), but not in syrphid density (37.8, 46.0 and 36.7 individuals seen per hour in the BG, FG, and HW respectively). Thus the null expectation is that dietary overlaps should be higher in HW (32 flower species) than in the BG (183 flower species).

Lists of hoverfly species in each site were analysed by using a technique similar to that of Connor & Simberloff (1978), developed by H. J. B. Birks and J. M. L. It compares the species diversity of the sites with that of the entire county of Cambridge, and tests whether the former can reasonably be regarded as random subsets of the county source pool. Sites are considered to be 'colonized' by a subset of all the syrphids that occur in the county. The actual number of species in common between two sites is compared with the number expected from random draws ('colonization'). Four different models of 'colonization' are used, differing according to the nature of the random sampling. Model I has equiprobable colonization, that is, all species have an equal chance of being drawn. Model II colonizes by weighting by the frequency of occurrence in sites (1/3, 2/3, or 3/3), a measure of colonizing ability (albeit rather poor: Connor & Simberloff 1978). In model III, weightings are derived from species abundances in the county (ranked and given a geometric score, 1, 2, 4, 8 or 16). Finally, in model IV, weightings are derived from frequencies in sites and abundances in the county. Only column totals (number of species in each site) are held constant in the simulations. Deviations are tested assuming a normal distribution. A list of the syrphids of Cambridgeshire, with their abundance scores, is given in appendix 1.

Morphometric analyses addressed two questions: (i) is the subset of species occurring in any one site subject to the ecological constraints of competition such that the observed proboscis-length ratios between adjacent rank-ordered species tend to be either larger than a minimum value, or constant? (ii) Have evolutionary forces tended to separate the proboscis lengths of potential competitors so that adjacent ratios of rank-ordered species tend to be greater than a certain minimum value, or be more constant than random expectation (Simberloff & Boecklen 1981). Measures of proboscis length are taken from Gilbert (1985a): we use both absolute proboscis length, and proboscis length relative to body size. The latter is represented by scores along the first axis of a canonical-variates analysis (see Gilbert 1985a).

We assume that ecological and evolutionary forces should be manifest between common species, and therefore analyse the 35 common species of Cambridgeshire for evolutionary trends, and the ten commonest species in each site (table 1) for ecological trends.

Ecological constraints upon the assemblage of communities that act through

TABLE 1. CLASSIFICATION OF THE 35 COMMONEST CAMBRIDGESHIRE HOVERFLIES, SHOWING THE TEN COMMONEST OF EACH SITE, THE MEAN PROBOSCIS LENGTHS, AND THE PROBOSCIS LENGTHS RELATIVE TO SIZE

(Relative proboscis length is represented by canonical variate means along the first axis of a canonical-variates analysis: see Gilbert (1985*a*). Nomenclature largely follows Stubbs & Falk (1983).)

subfamily, tribe, species	BG	site FG	HW	absolute length	relative length
Syrphinae					
Syrphini					
<i>Syrphus ribesii</i> L.	+	+	+	3.45	-5.9
<i>S. vitripennis</i> Mg.	.	.	.	2.99	-6.9
<i>Metasyrphus corollae</i> Fabr.	+	+	.	3.15	-3.3
<i>M. luniger</i> Mg.	.	.	.	3.35	—
<i>Scaeva pyrastris</i>	.	.	.	4.15	—
<i>Leucozona lucorum</i> L.	.	.	.	4.92	6.4
<i>Meliscaeva auricollis</i> Mg.	.	.	.	2.73	-8.0
<i>Episyrphus balteatus</i> deGeer	+	+	+	2.89	-9.5
<i>Sphaerophoria scripta</i> L.	+	.	.	3.44	—
Bacchini					
<i>Baccha obscuripennis</i> Mg.	.	.	.	1.64	-23.0
Melanostomatini					
<i>Melanostoma mellinum</i> L.	+	+	.	1.94	-10.3
<i>M. scalare</i> Fabr.	+	+	+	2.13	-11.3
<i>Platycheirus albimanus</i> Fabr.	+	+	+	3.42	2.4
<i>P. clypeatus</i> Mg.	.	+	.	2.13	-10.5
<i>P. manicatus</i> Mg.	.	.	+	4.89	10.4
<i>P. peltatus</i> Mg.	.	.	+	4.21	5.8
<i>P. scutatus</i> Mg.	.	.	.	2.93	-0.4
Eristalinae					
Pipizini					
<i>Pipiza austriaca</i> Mg.	.	.	+	2.02	-15.9
Cheilosini					
<i>Cheilosia paganus</i> Mg.	.	.	.	2.73	-1.0
<i>C. variabilis</i> Panzer	.	.	.	3.83	—
<i>Rhingia campestris</i> Mg.	.	.	.	10.53	27.4
<i>Ferdinandea cuprea</i> Scopoli	.	.	.	3.81	-2.8
Chrysogasterini					
<i>Neoscia podagrica</i> Fabr.	.	.	.	1.90	-5.3
Volucellini					
<i>Volucella bombylans</i> L.	.	.	.	7.82	11.8
<i>V. pellucens</i> L.	.	.	.	7.24	7.7
Xylotini					
<i>Xylota segnis</i> L.	.	.	+	2.59	-13.1
<i>X. sylvarum</i> L.	.	.	.	3.28	-14.7
<i>Syrirta pipiens</i> L.	+	+	.	3.44	4.0
Eristalini					
<i>Helophilus pendulus</i> L.	.	.	+	5.60	8.7
<i>Eristalis arbustorum</i> L.	+	.	.	5.43	8.3
<i>E. intricarius</i> L.	.	.	.	6.72	11.1
<i>E. nemorum</i> L.	.	.	.	6.07	10.8
<i>E. pertinax</i> Scopoli	.	.	+	6.44	7.0
<i>E. tenax</i> L.	+	+	.	7.75	11.7
<i>Myiatropa florea</i> L.	.	+	.	5.50	4.8

morphology (proboscis length, or relative proboscis length) are assessed by simulation. Comparisons are made between the observed parameters of the ten common species at a site, and values obtained from a random draw of ten species from the 35 commonest Cambridgeshire hoverflies. If regular spacing of proboscis length occurs, then the ratios of adjacent ranked proboscis lengths should be significantly more constant in the data from the sites than in the random samples. Constancy is assessed by taking the smallest (and second smallest) of the ratios, and dividing them by the largest; the figures thus obtained should be unusually high, if ratio constancy occurs (see Simberloff & Boecklen 1981).

The evolutionary question is assessed by converting the line-segment lengths between adjacent rank-ordered log-transformed proboscis lengths (see Simberloff & Boecklen 1981) to a distribution between 0 and 1 which, if spacings are random, should be similar to random draws from a uniform distribution. If spacings are regular, then the transformed spacings should cluster at some particular value. The transformation (see appendix 2) converts observed spacings ( $D_i$ ) into transformed spacings ( $T_i$ ) for  $n$  spacings in the range  $L$  between the shortest and longest proboscis, thus:

$$T_i = 1.0 - (1.0 - D_i/L)^n.$$

Evolutionary forces that act on proboscis length should be more evident between closely related species than among randomly picked species. We therefore look for evidence of minimum ratios and ratio constancy in congeneric species by comparing them with randomly selected 'genera' with the same number of species, that is, by simulation, in the same manner as for the ten species of each site (see above). Random 'genera' were created by drawing either from the full complement of 35 species, or from the relevant subfamily (17 or 18 species). Evidence for minimum ratios was gauged from the number of times in 100 runs that the simulated minimum ratio was less than the observed value. The congeneric species here are sympatric: if no evidence of differences exists, then comparison with allopatric congenics are precluded.

## RESULTS

Dietary overlaps in each site all show a broadly similar picture: the clustering of species in the Botanic Garden (figure 1) and Hayley Wood (figure 2) show the patterns obtained. Taxonomically related species have similar diets both in terms of the flowers that they visit and the food that they take from the flower (nectar or pollen). The two commonest species, *E. balteatus* and *S. ribesii*, are closely related and have very similar diets. Overlaps from the BG (many flowers) are much lower than those of HW (few flowers), as expected. Clusters contain similar groups. The two *Xylota* species are separated because they rarely or never visit flowers, but specialize in collecting material from leaf-surfaces (Gilbert 1985*b*). These data suggest two things: competition, if it occurs, should be strongest between closely related species, since they visit similar types of flower; and competition has not caused divergence in visiting patterns.

Species composition of the sites show some interesting features (table 2). For both the more elaborate models (III and IV) that include species abundances in

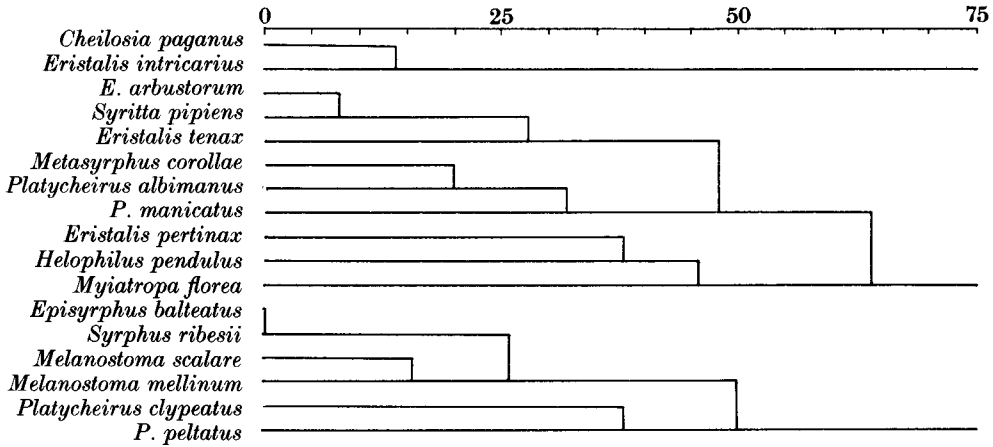


FIGURE 1. Results of cluster analysis of dietary overlaps from the Botanic Garden site. The two main divisions are separated on the basis of the food the species take from the flowers; one group contains species mainly feeding on pollen (for example, *Syrphus ribesii*), and the other species taking nectar and pollen (for example, *Syrritta pipiens*).

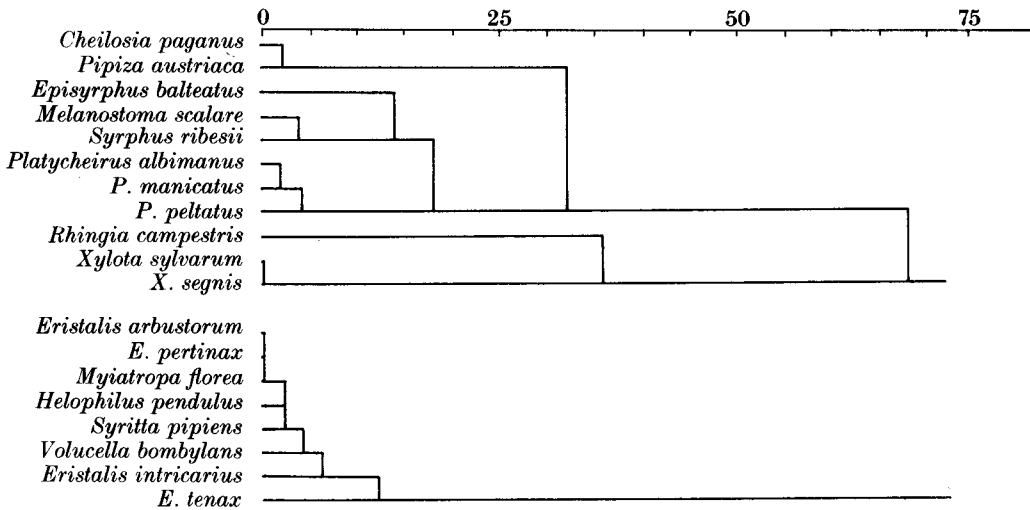


FIGURE 2. Results of cluster analysis of dietary overlaps from the Hayley Wood site. Note the similarity in the main clusters to figure 1.

the county source pool, the ancient woodland site has significantly fewer species in common with the urban sites than expected from random colonization. No differences were detected between the urban sites. We interpret these results as indicating that, within the constraints of the models, communities in the urban sites cannot be distinguished from random collections of Cambridgeshire hoverflies, whereas the woodland community cannot be viewed as a random assemblage.

How are species selected from the Cambridgeshire source-pool in the three sites, morphologically speaking? Table 3 shows the results of the analyses. The urban

TABLE 2. RESULTS OF THE ANALYSIS OF SPECIES COMPOSITION, COMPARING SPECIES IN COMMON BETWEEN PAIRS OF SITES WITH RANDOM EXPECTATION FROM A COLONIZATION OF THE SITES FROM THE COUNTY POOL OF SPECIES

		pairwise site comparisons		
		BG-FG	FG-HW	BG-HW
observed species in common		36	34	30
model†				
I	expected‡, ¶	13.91	16.89	13.91
	deviation§	+8.47*	+6.20*	+6.17*
II	expected	31.53	38.18	31.94
	deviation	+2.37*	-2.29*	+1.12
III	expected	34.24	40.59	34.10
	deviation	+0.94	-3.96*	-2.31*
IV	expected	36.76	42.93	36.75
	deviation	-0.50	-4.28*	-5.40*

† Model I, species have equal probabilities of colonizing sites. Model II, colonization weighted by frequency of occurrence in the sites, that is, by 1/3, 2/3, or 3/3. Model III, colonization weighted by relative abundances of species in the source pool; species were scored in five abundance categories and given an abundance score on a geometric scale, that is, 1, 2, 4, 8 or 16. Model IV, colonization weighted by both the relative abundances in the source pool and the frequency of occurrence in the sites.

‡ Calculated from 250 iterations of random sampling in models II, III, and IV; model I is deterministic, and does not involve simulation.

§ Calculated from (Observed - Expected)/(s.d.), where s.d. is the standard deviation of the expected number from the random sampling.

¶ Number of sites, 3; number of species in source pool, 154; number of species in at least one site, 72. For a list of Cambridgeshire hoverflies and their abundances see Appendix.

\* Significant at the 5% level, assuming the deviations follow a normal distribution.

sites show no evidence of ratio constancy: in fact the BG has a significantly large difference between the smallest and largest ratio ( $P < 0.05$ ). The ancient woodland (HW), on the other hand, has a significantly low ratio variance ( $P < 0.01$ ), indicating that the ten commonest species tend to have constant ratios of proboscis lengths. No site shows significantly large minimum ratios.

Table 1 gives the proboscis lengths for all common or moderately common species in Cambridgeshire. A plot of the ranks against logarithm of proboscis length gives a distribution expected for random draws from a uniform distribution (mean,  $1.33 \pm 0.46$ ,  $n = 35$ ; coefficient of skewness,  $0.22 \pm 0.40$ ; coefficient of kurtosis,  $\beta_2 = 2.31 \pm 0.78$ ). The distribution of transformed spacings (figure 3) shows that there are many small ( $T_1 < 0.35$ ) and medium to large ratios ( $T_1 > 0.5$ ). There is no evidence for regularity of ratios (that is, a clustering of values) or for a minimum ratio.

Congeneric species show interesting patterns (table 4). Observed minimum ratios are not particularly large, because they show no significant differences at the 5% level from random expectation, although some comparisons approach significance (*Metasyrphus*,  $P < 0.06$ ; *Melanostoma* and *Volucella*,  $0.1 > P > 0.05$ ). However,



TABLE 3. ANALYSIS OF THE MORPHOLOGICAL SPACING OF THE TEN COMMONEST SPECIES OF EACH SITE, COMPARED WITH RANDOM DRAWS OF TEN SPECIES FROM THE 35 COMMONEST CAMBRIDGESHIRE HOVERFLIES

site	observed variance	NVAR	observed $G_{19}$	$G_{19}^N$	observed $G_{29}$	$G_{29}^N$
BG	0.005	81.6	0.0	95.2	0.006	98.8
FG	0.005	81.4	0.006	74.2	0.019	94.2
HW	0.0006	0.8	0.059	20.4	0.266	18.4

NVAR, percentage of 500 runs where simulated variance was less than the observed variance.

$G_{19}^N$ , percentage of 500 runs where simulated  $G_{19}$  (obtained by dividing the smallest difference between ranked log-transformed proboscis lengths by the largest for the ten species) was greater than the observed  $G_{19}$ .

$G_{29}^N$ , percentage of 500 runs where simulated  $G_{29}$  (obtained by dividing the second smallest difference between ranked log-transformed proboscis lengths by the largest for the ten species) was greater than the observed  $G_{29}$ .

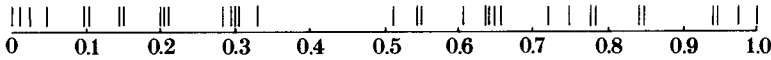


FIGURE 3. Plot of the transformed spacings ( $T_i$ ). If actual spacings ( $\log(\text{proboscis length})_i - \log(\text{proboscis length})_j$ ) have a randomly distributed magnitude, then the transformed spacings should be randomly distributed between 0 and 1. If spacings tend to have some particular value, then the transformed spacings should be clustered around a point.

seven of the eight genera show ratios greater than the random median of 50% ( $P < 0.032$ , one-tailed test), suggesting some tendency towards separation of proboscis length in congenetics. Of the two genera with more than two members, *Eristalis* shows clear evidence of constancy of ratios, with both  $G_{14}$  and the variance being significantly different from random expectation ( $P < 0.02$  in both cases). It is interesting to note that *Eristalis* spp. feed predominantly on nectar (Gilbert 1981*b*) and might therefore be more likely to show evidence of competitively moulded proboscis lengths than species that take much more pollen in their diets (such as *Syrphus* and to a lesser extent *Platycheirus*), if competition were an important factor in adult hoverfly biology. In *Platycheirus*, *P. clypeatus* feeds almost exclusively upon pollen (van der Goot & Grabandt 1970; Gilbert 1985*b*), whereas other members of the genus are much more often seen taking nectar (35–50% of observations: Gilbert 1985*b*). Exclusion of *P. clypeatus* results in ratios significantly more constant than random expectation (source pool 35 species,  $P < 0.02$ ; source pool 17 (Syrphinae),  $P < 0.05$ ). These constant ratios could be due to ecological forces over evolutionary time, or simply due to a lack of divergence from the common ancestor, that is, a result of weak selective forces. In the case of *Platycheirus*, proboscis lengths relative to the body size are sufficiently different for the latter to be unlikely.

Syrphids vary greatly in size (250-fold mass difference between the smallest and largest), and therefore in their energetic requirements. Since deeper corollae contain more energy in the form of nectar (Prÿs-Jones 1982), it can be argued that the important parameter in syrphid feeding is proboscis length relative to body

TABLE 4. TESTS ON THE PROBOSCIS-LENGTH RATIOS BETWEEN ADJACENT SIZE-ORDERED SPECIES: TESTS FOR MINIMUM SIZE RATIOS ( $G_1^N$ ) AND CONSTANT SIZE RATIOS ( $G_{14}^N$ )

genus	$S$	$N$	comparison with random draws			
			absolute length		relative length	
			$G_1^N$	$G_{14}^N$	$G_1^N$	$G_{14}^N$
<i>Syrphus</i>	2	35	85.0	—	94.0	—
		17	77.6	—	89.0	—
<i>Metasyrphus</i>	2	35	94.5	—	—	—
		17	90.5	—	—	—
<i>Melanostoma</i>	2	35	91.3	—	95.0	—
		17	82.3	—	96.0	—
<i>Platycheirus</i>	5	35	15.3	8.4	16.0	18.0
		17	8.6	19.6	11.0	19.0
	4	35	40.0	1.6	33.0	5.0
		17	—	—	35.0	4.0
<i>Cheilosia</i>	2	35	66.2	—	—	—
		18	71.4	—	—	—
<i>Volucella</i>	2	35	93.1	—	78.0	—
		18	92.3	—	75.0	—
<i>Xylota</i>	2	35	74.4	—	92.0	—
		18	77.8	—	93.0	—
<i>Eristalis</i>	5	35	62.8	1.6	98.0	40.0
		18	64.5	1.1	91.0	39.0

For those genera with more than one species, the smallest size ratio ( $G_1$ ) was compared with the smallest size ratio in a random set of  $S$  species drawn from  $N$  species, either the full complement of 35 species, or the subfamily containing the genus (17 or 18 species).  $G_1^N$  gives the percentage of runs where the observed  $G_1$  was greater than the randomly drawn  $G_1$ . For the two genera with five species, the ratio of the smallest to the largest,  $G_{14}$ , was computed, and compared with similar random values:  $G_{14}^N$  gives the percentage of runs where the observed  $G_{14}$  was greater than the randomly drawn  $G_{14}$ . Relative proboscis lengths were represented by the mean scores along the first canonical axis of a canonical-variates analysis (Gilbert 1985a).

size. We therefore have repeated the analysis using canonical variate means along the first canonical axis as an estimate of relative proboscis length (Gilbert 1985a: data in table 1). Only the evolutionary question was addressed.

The distribution of ranked spacings for the 35 species common in Cambridgeshire was again not significantly different from that expected of random draws from a uniform distribution (mean,  $-0.16 \pm 10.87$ ; coefficient of skewness,  $0.11 \pm 0.42$ ; coefficient of kurtosis,  $\beta_2 = 2.82 \pm 0.82$ ). There is no evidence for constant or minimum differences, with the pattern being very similar to figure 3. There are no indications that differences in canonical variate scores between congenics are larger than some minimum value ( $P > 0.11$ : table 3). However, although individual comparisons are not significant, in five out of the six comparisons the smallest difference in canonical variate score relative to the largest was greater than random expectation ( $0.05 < P < 0.1$ , one-tailed test). As for proboscis length, this suggests

a tendency for congeneric species to have rather more separated canonical variate scores than randomly drawn species. There was no evidence for constant score differences between congenics in *Platycheirus* or *Eristalis* ( $P > 0.18$  in both cases), but there was clear statistical evidence for constant differences in *Platycheirus* when *P. clypeatus* was omitted from the analysis ( $P < 0.05$ : see above for rationale).

#### DISCUSSION

The notion that distributional and ecological relationships between closely related species has been strongly influenced by competition has been a controversial issue for many years. Williams (1947, 1951) pointed out that such a view is open to statistical testing. His null hypothesis concerning the distribution of congeneric as opposed to intergeneric species, far from being rejected when tested with East African birds suggested that patterns accorded with the opposite of what was expected. Instead of indicating a 'principle of competitive exclusion', his results argue for a 'principle of coexistence': closely related species are more often found coexisting than is predicted from random models. Simberloff (1970), Kikkawa (1977), Birch (1979) and den Boer (1980) support this contention. In syrphids, closely related species have very similar patterns of resource use, and these similarities occur in all sites. Species should segregate their niches in this way, even if resources are not limiting, because selection for individual efficiency still occurs (Hespenheide 1973; Thomson 1980). Significant resource partitioning, in fact, can be documented almost anywhere, even between conspecific individuals of the same sex (den Boer 1980).

Morphological approaches to community structure are not common in the literature, especially multivariate treatments (Ricklefs & Travis 1980; Ricklefs *et al.* 1981). In the syrphid community, closely related species have more similar diets than distantly related ones (see also Gilbert 1985*b*). This makes it difficult to demonstrate the causal effects of competition for food on morphological divergence.

Analysis of species composition in three sites has demonstrated that the community of hoverflies in ancient woodland cannot be regarded as having been derived from random colonization from the county source-pool, given the model assumptions. The differences between tests for ratio constancy in each site lend support to this interpretation. Recent man-made habitats contain species assemblages indistinguishable from random collections.

Size and shape covary (Mosimann & James 1970; Alberch *et al.* 1979), and there is no reason to suspect selection for size and not shape, no vice versa; observed size changes may on the other hand be epiphenomena of selection for shape (Simberloff & Boecklen 1981). In organisms that forage from flowers, there are *a priori* reasons for focusing attention on the mouthparts, and previous analyses have demonstrated the link between morphology and ecology in syrphids (Gilbert 1985*a, b*). It is interesting to note that in the two genera with adequate numbers of species for the test, *Platycheirus* and *Eristalis*, both show evidence of constant ratios of proboscis lengths. In the case of *Eristalis*, these appear to be consequences of size differences because they have abnormally small differences in relative

proboscis length (table 4). In *Platycheirus*, the species differ in shape as well as size; those species which feed on nectar have constant proboscis length ratios, and constant differences in relative proboscis length too.

There are many more short-tongued syrphids than there are long-tongued ones (F. S. Gilbert, unpublished data); bee-flowers have a skewed distribution of corolla depth (Inouye 1978*b*; Prÿs-Jones 1982), and presumably those visited by hoverflies do too. If the Syrphidae evolved from a short-tongued ancestor, as seems likely (Hull 1949; Röder 1980), one can imagine random increases in size and proboscis length, or both (cf. Alberch *et al.* 1979). If such mutations were relatively uncommon, such a model might produce a skewed distribution of proboscis length. The immediate advantage given to species with a longer proboscis is that it allows a shifting of the niche, without implying competitively based selection, permitting nectar to be obtained from flowers with deeper corollae, which contain more nectar (Brink & de Wet 1980; Prÿs-Jones 1982). The lengthening of the proboscis is very often associated with general size increase, hence an increase in the absolute energy requirements: larger body size is associated with the switch from pollen to nectar feeding (Gilbert 1985*b*). Primitive hoverflies were almost certainly pollen feeders.

We have shown that adult hoverflies partition resources, with more closely related species having similar diets; and that species composition is non-random (with respect to a colonization model, with the county list as source-pool) for a relatively undisturbed site, but random for two man-made habitats. Morphological analyses support this result, in that proboscis-length ratios between adjacent rank-ordered species are significantly constant in the undisturbed site, but not in the other sites. One reason for this might be the competitive structuring envisaged by the theory of species packing (Hutchinson 1978).

However, we have deliberately ignored the role of complex life-cycles in our analysis. The composition of syrphid communities is as likely to be influenced by larval as by adult ecology. The overwhelming numerical superiority of species with aphidophagous larvae is probably a reflection of the availability of their prey. It seems likely that competition occurs between larvae in a colony of aphids, since colonies are frequently obliterated by predation; starvation in larvae causes a loss of reproductive potential (Cornelius & Barlow 1980), and in years when there are fewer aphids than usual, there appears to be a higher frequency of 'starvation dwarf' adults (personal observation). All the common aphidophagous species have larvae that can feed and complete metamorphosis on a wide variety of aphids (Růžička 1976; Růžička & Cairo 1976). Studies of predatory behaviour in larvae have recently been published (see Rotheray 1983), and surveys of and experiments with larval communities are under way.

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## REFERENCES

- Abrams, P. 1976 Limiting similarity and the form of the competition coefficient. *Theoret. Pop. Biol.* **8**, 356–375.
- Aho, J., Ranta, E. & Vuorinen, J. 1981 Species composition of freshwater snail communities in lakes of southern and western Finland. *Ann. Zool. Fenn.* **18**, 233–241.
- Alberch, P., Gould, S. J., Oster, G. F. & Wake, D. B. 1979 Size and shape in ontogeny and phylogeny. *Paleobiology* **5**, 296–317.
- Birch, L. C. 1979 The effect of species of animals which share common resources on one another's distribution and abundance. *Fortschr. Zool.* **25**, 197–222.
- den Boer, P. J. 1980 Exclusion or coexistence and the taxonomic or ecological relationship between species. *Neth. J. Zool.* **30**, 278–306.
- Bowers, M. A. & Brown, J. H. 1982 Body size and coexistence in desert rodents: chance or community structure? *Ecology* **63**, 391–400.
- Brink, D. & de Wet, J. M. J. 1980 Interpopulation variation in nectar production in *Aconitum columbianum* (Ranunculaceae). *Oecol., Berl.* **47**, 160–163.
- Brown, J. H., Calder, W. A. & Kodric-Brown, A. 1978 Correlates and consequences of body size in nectar-feeding birds. *Am. Zool.* **18**, 687–700.
- Carpenter, F. L. & MacMillen, R. E. 1976 Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science, Wash.* **194**, 639–642.
- Chernov, Y. 1966 The complex of anthophilous insects in the tundra zone. *Voprosy geografii* **69**, 76–97. (In Russian.)
- Connor, E. F. & Simberloff, D. 1978 Species number and compositional similarity of the Galapagos fauna and flora. *Ecol. Monogr.* **48**, 219–248.
- Connor, E. F. & Simberloff, D. 1983 Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. *Oikos* **41**, 455–465.
- Cornelius, M. & Barlow, C. A. 1980 Effect of aphid consumption by larvae on development and reproductive efficiency of a flower fly, *Syrphus corollae* (Diptera, Syrphidae). *Can. Ent.* **112**, 989–992.
- Diamond, J. M. & Gilpin, M. E. 1982 Examination of the 'null' model of Connor and Simberloff for species co-occurrences on islands. *Oecol., Berl.* **52**, 64–74.
- Ewald, P. W. 1980 Energetics of resource defence: an experimental approach. In *Acta XVII Int. Congr. Ornith., Berlin 1978* (ed. R. H. Nöhring), pp. 1093–1099.
- Gilbert, F. S. 1981 Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecol. Ent.* **6**, 245–262.
- Gilbert, F. S. 1985a Morphometric patterns in hoverflies (Diptera, Syrphidae). *Proc. R. Soc. Lond. B* **224**, 79–90.
- Gilbert, F. S. 1985b Ecomorphological relationship in hoverflies (Diptera, Syrphidae). *Proc. R. Soc. Lond. B* **224**, 91–105.
- Gill, F. B. 1978 Proximate costs of competition for nectar. *Am. Zool.* **18**, 753–763.
- Gill, F. B. & Wolf, L. L. 1975 The economics of feeding territoriality in the golden-winged sunbird. *Ecology* **56**, 333–334.
- van der Goot, V. S. & Grabandt, R. A. J. 1970 Some species of the genera *Melanostoma*, *Platycheirus* and *Pyrophaena* (Diptera, Syrphidae) and their relation to flowers. *Ent. Ber., Amst.* **30**, 135–143.
- Harvey, P. H., Colwell, R. W., Silvertown, J. G. & May, R. M. 1983 Null models in ecology. *Ann. Rev. Ecol. Syst.* **14**, 189–212.
- Heinrich, B. 1976 Resource partitioning among some eusocial insects: bumblebees. *Ecology* **57**, 874–889.
- Hespenheide, H. A. 1973 Ecological inferences from morphological data. *Ann. Rev. Ecol. Syst.* **4**, 213–229.
- Hippa, H., Koponen, S. & Osmonen, O. 1981 Pollen transport and pollinating efficiency of flower visitors to the cloudberry (*Rubus chamaemorus* L.) in northern Fennoscandia. *Rep. Kevo Subarctic Res. Stat.* **17**, 58–66.
- Högstedt, G. 1980 Prediction and test of the effects of interspecific competition. *Nature, Lond.* **283**, 64–66.
- Hull, F. M. 1949 The morphology and interrelationships of the genera of Syrphid flies, recent and fossil. *Trans. zool. Soc. Lond.* **26**, 257–408.

- Hutchinson, G. E. 1959 Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159.
- Hutchinson, G. E. 1978 *An introduction to population ecology*. New Haven: Yale University Press.
- Inouye, D. W. 1978a Resource partitioning in bumblebees: experimental studies of foraging behaviour. *Ecology* **59**, 672–678.
- Inouye, D. W. 1978b Patterns of corolla tube length of bumblebee flowers. *Spec. Misc. Publ. Maryland agric. exp. Stat.* **1**, 461–463.
- Karr, J. R. & James, F. C. 1975 Eco-morphological configurations and convergent evolution in species and communities. In *Ecology and evolution of communities* (ed. M. L. Cody & J. M. Diamond), pp. 258–291. Cambridge: Belknap Press.
- Kikkawa, J. 1977 Ecological paradoxes. *Austr. J. Ecol.* **2**, 121–136.
- Løvtrup, S. 1977 Derek Roff and the evolution of body size: a rejoinder. *Evol. Theory* **3**, 155–157.
- Løvtrup, S., Rahemtulla, F. & Höglund, N. G. 1974 Fisher's axiom and the body size of animals. *Zool. Scripta* **3**, 53–58.
- Maiorana, V. C. 1978 An explanation of ecological and developmental constants. *Nature, Lond.* **273**, 375–377.
- Montgomery, R. D. & Gass, C. L. 1981 Energy limitation of hummingbird populations in tropical and temperate communities. *Oecol., Berl.* **50**, 162–165.
- Mosimann, J. E. & James, F. C. 1979 New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution* **33**, 444–459.
- Orlaci, L. 1967 An agglomerative method for classification of plant communities. *J. Ecol.* **55**, 193–206.
- Pacala, S. & Roughgarden, J. 1982 Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science, Wash.* **217**, 444–446.
- Prÿs-Jones, O. E. 1982 Aspects of the life-history and foraging ecology of bumblebees. Unpublished Ph.D. Thesis, Cambridge University.
- Rackham, O. 1975 *Hayley Wood*. Cambridge: Cambridgeshire & Isle of Ely Naturalists' Trust.
- Ranta, E. & Lundberg, H. 1980 Resource partitioning in bumblebees: the significance of differences in proboscis length. *Oikos* **35**, 298–302.
- 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., Cochran, D. & Pianka, E. R. 1981 A morphological analysis of the structure of communities of lizards in desert habitats. *Ecology* **62**, 1474–1483.
- Ricklefs, R. E. & Travis, J. 1980 A morphological approach to the study of avian community organisation. *Auk* **97**, 321–338.
- Röder, G. 1980 A new *Cheilosia* species from Baltic amber, with SEM-studies of recent species. *Stutt. Beitr. Naturk. (Ser. B)* **64**, 1–18. (In German.)
- Roth, V. L. 1979 Can quantum leaps in body size be recognised among mammalian species? *Paleobiology* **5**, 318–336.
- Roth, V. L. 1981 Constancy in the size ratios of sympatric species. *Am. Nat.* **118**, 394–404.
- Rotheray, G. E. 1983 Feeding behaviour of *Syrphus ribesii* and *Metasyrphus corollae* on *Aphis fabae*. *Ent. exp. appl.* **34**, 148–154.
- Růžička, Z. 1976 The effect of various aphids as larval prey on the development of *Metasyrphus corollae* (Dipt., Syrphidae). *Entomophaga* **20**, 393–402.
- Růžička, Z. & Cairo, V. G. 1976 The effect of larval starvation on the development of *Metasyrphus corollae* (Diptera). *Vest. cesk. spol. zool.* **40**, 206–213.
- Schoener, T. W. 1970 Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**, 408–418.
- Simberloff, D. S. 1970 The taxonomic diversity of island biotas. *Evolution* **24**, 22–47.
- Simberloff, D. S. 1978 Using island biogeographic distributions to determine if colonisation is stochastic. *Am. Nat.* **112**, 713–726.
- Simberloff, D. S. 1983 Biogeography: the unification and maturation of a science. In *Perspectives in ornithology* (ed. A. H. Brush & G. A. Clarke), pp. 411–455. Cambridge: University Press.
- Simberloff, D. S. & Boecklen, W. 1981 Santa Rosalia reconsidered: size ratios and competition. *Evolution* **35**, 1206–1228.
- Strong, D. R. 1980 Null hypotheses in ecology. *Synthese* **43**, 271–285.

- Stubbs, A. E. & Falk, S. 1983 *British hoverflies*. London: British Entomological and Natural History Society.
- Thomson, J. D. 1980 Implications of different sorts of competition. *Am. Nat.* **116**, 719–726.
- Wiens, J. A. 1977 On competition in variable environments. *Am. Sci.* **65**, 590–597.
- Wiens, J. A. 1982 On size ratios and sequences in ecological communities: are there no rules? *Acta Zool. Fenn.* **19**, 297–308.
- Wiens, J. A. 1983 Avian community ecology: an iconoclastic view. In *Perspectives in ornithology* (ed. A. H. Brush & G. A. Clarke), pp. 355–402. Cambridge: University Press.
- Wiens, J. A. & Rotenberry, J. T. 1980 Patterns of morphology and ecology in grassland and shrubsteppe bird populations. *Ecol. Monogr.* **50**, 287–308.
- Wiens, J. A. & Rotenberry, J. T. 1981 Morphological size ratios and competition in ecological communities. *Am. Nat.* **117**, 592–599.
- Williams, C. B. 1947 The generic relations of species in small ecological communities. *J. anim. Ecol.* **16**, 11–18.
- Williams, C. B. 1951 Intra-generic competition as illustrated by Moreau's records of East African bird communities. *J. Anim. Ecol.* **20**, 246–253.

APPENDIX 1. LIST OF SYRPHIDS OF CAMBRIDGESHIRE WITH  
THEIR RELATIVE ABUNDANCES

(I. Perry, unpublished data. Numbers refer to relative abundances as used in the random models: 1, under 5 records; 2, rare; 4, uncommon; 8, common, 16 abundant; 32, superabundant.)

*Baccha* spp. (8), *Melanostoma mellinum* (16), *M. scalare* (32), *Platycheirus albimanus* (32), *P. ambiguus* (4), *P. angustatus* (1), *P. clypeatus* (8), *P. discimanus* (1), *P. fulviventris* (4), *P. immarginatus* (1), *P. manicatus* (16), *P. peltatus* (16), *P. scutatus* (16), *P. tarsalis* (2), *Pyrophaena granditarsa* (4), *P. rosarum* (4), *Xanthandrus comtus* (1), *Paragus haemorrhous* (1), *Chrysotoxum bicinctum* (1), *C. cautum* (4), *C. elegans* (1), *C. festivum* (1), *C. verralli* (1), *Dasysyrphus albostrigatus* (8), *D. lunulatus* (1), *D. tricinctus* (2), *D. venustus* (4), *Didea fasciata* (1), *Epistrophe eligans* (8), *E. grossulariae* (4), *E. nitidicollis* (1), *Epistrophe euechroma* (1), *Episyrphus balteatus* (32), *Leucozona laternarius* (1), *L. lucorum* (8), *Melangyna barbifrons* (1), *M. cincta* (1), *M. guttata* (1), *M. labiatarum* (4), *M. lasiophthalma* (4), *M. quadrimaculata* (1), *M. triangulifera* (1), *M. umbellatarum* (4), *Meliscaeva auricollis* (8), *M. cinctella* (8), *Metasyrphus corollae* (32), *M. latifasciatus* (1), *M. luniger* (8), *Parasyrphus punctulatus* (4), *Scaeva pyrastris* (8), *S. selenitica* (2), *Sphaerophoria abbreviata* (1), *S. menthastri* (1), *S. rueppelli* (2), *S. scripta* (16), *Syrphus ribesii* (32), *S. torvus* (2), *S. vitripennis* (32), *Xanthogramma citrofasciatum* (1), *X. pedissequum* (2), *Callicera spinolae* (2), *Cheilisia albipila* (2), *C. albitarsis* (4), *C. bergenstammi* (1), *C. cynocephala* (1), *C. fraterna* (4), *C. grossa* (4), *C. honesta* (2), *C. illustrata* (8), *C. impressa* (4), *C. intonsa* (1), *C. longula* (1), *C. nebulosa* (2), *C. paganus* (8), *C. praecox* (2), *C. proxima*, species D of Stubbs & Falk (4), *C. pubera* (1), *C. scutellata* (1), *C. semifasciata* (1), *C. soror* (1), *C. variabilis* (8), *C. vernalis* (8), *C. vulpina* (1), *Ferdinandea cuprea* (4), *Portevinia maculata* (2), *Rhingia campestris* (8), *Brachyopa insensilis* (2), *B. scutellaris* (4), *Chrysogaster hirtella* (8), *C. solstitialis* (4), *Lejogaster metallina* (2), *L. splendida* (1), *Myolepta luteola* (1), *Neoascia aenea* (1), *N. tenur* (4), *N. geniculata* (1), *N. podagrica* (16), *Orthoneura brevicornis* (1), *O. geniculata* (2), *O. nobilis* (1), *O. splendens* (4), *Sphegina clunipes* (2), *S. kimakowczy* (1), *Anasimyia lineata* (1), *A. interpunctata* (2), *A. transfuga* (2), *Eristalinus aeneus* (1), *E. sepulchralis* (4), *E. arbustorum* (8), *E. horticola* (4), *E. intricarius* (8), *E. nemorum* (4), *E. pertinax* (16),

*E. tenax* (16), *Helophilus hybridus* (4), *H. paralellus* (2), *H. pendulus* (16), *Mallota cimbiciformis* (1), *Myiatropa florea* (8), *Parhelophilus frutetorum* (1), *P. versicolor* (4), *Eumerus ornatus* (1), *E. strigatus* (8), *E. tuberculatus* (2), *Merodon equestris* (4), *Heringia heringii* (1), *Neocnemodon pubescens* (1), *N. verrucula* (1), *N. vitripennis* (2), *Pipiza austriaca* (4), *P. fenestrata* (2), *P. luteitarsis* (4), *P. noctiluca* (8), *Pipizella varipes* (4), *P. virens* (2), *Trichopsomyia flavitarsis* (2), *Triglyphus primus* (1), *Sericomyia silentis* (1), *Volucella bombylans* (8), *V. inflata* (1), *V. pellucens* (8), *Chalcosyrphus nemorum* (2), *Criorhina asilica* (1), *C. berberina* (1), *C. floccosa* (2), *Pocota personata* (1), *Syritta pipiens* (32), *Tropidia scita* (4), *Xylota abiens* (2), *X. segnis* (8), *X. sylvarum* (4), *X. tarda* (1).

Other records: *Cheilosia griseiventris* (1), *C. proxima*, species E of Stubbs & Falk (4), *Anasimyia contracta* (4), *Pipiza bimaculata* (4), *Xylota florum* (1).

## APPENDIX 2

We consider a hypothesis that the original data are uniformly scattered at random on (0, 1). This implies that the spacing  $Y$  between adjacent data points has a distribution given by

$$P[Y > x] = (1-x)^n \quad \text{for } 0 < x < 1.$$

Hence

$$P[Y < x] = 1 - (1-x)^n. \quad (1)$$

If

$$u = 1 - (1-y)^n$$

then

$$\begin{aligned} P[U \leq u] &= P[1 - (1-Y)^n \leq u] \\ &= P[(1-Y)^n \geq 1-u] \\ &= P[1-Y \geq (1-u)^{1/n}] \\ &= P[Y \leq 1 - (1-u)^{1/n}]. \end{aligned} \quad (2)$$

Substituting for  $x$  in (1),

$$\begin{aligned} P[Y \leq x] &= 1 - \{1 - [1 - (1-u)^{1/n}]\}^n \\ &= u, \text{ which means that } U \text{ is uniformly distributed on } (0, 1). \end{aligned}$$

Hence the effect of the transform  $y \rightarrow u$  is to convert the non-uniform distribution of  $Y$  into a uniform distribution of  $U$ , if the hypothesis is correct.