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Spatial distribution of bibionid larvae in agricultural grassland

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Abstract

The distribution of bibionid larvae in agricultural grassland was investigated. They tend to occur sporadically and at low population density. More detailed sampling within a field showed that numbers were highest adjacent to a hedgerow with most being found 6–11 m from the hedge. Log variance/log mean relationships were established for counts of *Bibio johannis* and *Dilophus febrilis* larvae collected from soil cores in grassland. Both species were highly aggregated. An area of grassland (160 cm × 80 cm) was divided into 128 soil blocks and *B. johannis* larvae extracted. Almost all larvae were associated with aggregations. The two-phase mozaic method of Pielou (1974) was applied to larval counts from different sized concentrically collected soil cores. Larval patches were not randomly distributed. Time-lapse video studies of bibionid larvae were made and showed both aggregation and processional behaviour. This was associated with chemical stimulation which is probably used to maintain larval groupings in the field. There was evidence for two levels of aggregation. The first is due to groups of larvae arising from eggs laid by a single female and the second, larger scale, aggregation is due to factors that influence the distribution of adult flies.

Introduction

Bibionid larvae are soil dwellers and primarily feed on decaying organic matter but will consume living plant material when decaying matter is exhausted, so are best described as phyto-saprophagous (Pecina, 1982). As a result they can be occasional pests of a wide range of agricultural and horticultural crops (D'Arcy-Burt & Blackshaw, 1991). Most species have an annual life-cycle although some, e.g. *Dilophus febrilis* (L.), have two flight periods each year (Blackshaw & D'Arcy-Burt, 1992).

The presence of organic materials, such as manures and slurries, are thought to be important to the distribution of bibionids and may be correlated with large numbers of larvae (Vorsatz & Rode, 1967). There is also evidence (Dawson, 1932; Lovibond, 1938; MacDougall, 1932) that adults are attracted to manure to lay their eggs. Rotting or fermenting crop remains such as straw stubble, pea haulm or sugar beet crowns may also provide preferred oviposition sites (Muller, 1932). After mating, females burrow into the soil and form an oviposition chamber where 200–400 eggs are produced. Larvae complete their development in the soil.

Factors influencing the occurrence of bibionids in farm land are not understood and have received little attention, although published references to bibionid larvae comment on their occurrence in dense clumps in the soil (e.g. Colyer & Hammond, 1968; Freeman & Lane, 1985) – a facet of bibionid biology that has not previously been studied. This paper reports an investigation into aspects of the spatial distribution and aggregation of bibionid larvae in grassland.

Materials and methods

All larvae in experiments were recovered from soil by wet-sieving and salt flotation (Blackshaw & D'Arcy-Burt, 1993).

Distribution between fields. Samples of 60 soil cores were taken from grass fields at four different locations (Newforge Lane, Belfast, Grid ref. J334370; Ballyharvey Farm, Antrim, Grid ref. J176846; Loughgall, Armagh, Grid ref. H292352; Hillsborough, Down, Grid ref. J325358) between 8–13 October 1984. Further samples were taken from 5 grass fields at Ballyharvey Farm from 15–20 October 1984 and from 8 sub-sections of Lower Ram field, Ballyharvey Farm from 29 October – 3 November 1984. All cores were collected using stratified random sampling.

Distribution along a hedgerow. A rectangular lattice of six rows of 12 points was marked out parallel to a hedge in Lower Ram field at distances of 1, 6, 11, 16, 21 and 25 m from a boundary edge. Each of the points in a row was spaced 5 m apart giving an array of 72 sampling points over an area 55 × 25 m. A portable square grid divided into 16 squares of 15 × 15 cm was placed centrally on each sampling point in turn. The 16 squares were randomly allocated to a sampling sequence unique to each sampling point. A soil core was taken from the centre of the appropriate square on each sampling occasion. Sampling commenced on 9 November 1984 and continued fortnightly until 22 March 1985. On 18 January 1985 the soil was frozen and no sample was collected.

Variation in the total number of bibionid larvae recovered from samples was analysed for sampling date, columns, rows and their interactions.

Variance/mean relationship. Soil samples were collected fortnightly from grassland in Lower Ram Field at Ballyharvey Farm, Antrim (Irish grid ref. J170856) from June 1985 to March 1987. Each sample consisted of 60 cores (10 cm diameter and 8 cm depth). The numbers of larvae (*Bibio johannis* (L.) and *D. febrilis*) recovered were recorded for each core and the sample mean and variance calculated prior to a log-log regression to establish an index of aggregation (Taylor, 1961, 1971).

Complete enumeration. An area of 128 (16 × 8) square contiguous blocks ($= 1\cdot 28\ \mathrm{m}^2$) was marked out at lower Ram Field and the vegetation clipped to the ground. Each block was cut out to a depth of 10 cm with a sharp steel blade, removed and individually bagged and labelled.

Two-phase mosaics. Many indices of aggregation are concerned with the distribution of individuals but it is also useful to have a measure of the pattern of patches of individuals separated by gaps where no individuals occur. Pielou (1964) described this type of pattern as a 'two-phase mosaic' and developed a method of testing whether the two phases (patches and gaps) were randomly mingled.

The minimum distance between two individuals that constitutes a gap can be defined as **r** so that any two individuals that are separated by a distance less than **r** will be within a patch and any by greater than **r** will be in two distinct patches. If circular sampling units of radius **r** are used to sample a population, units containing at least one individual can be scored as a 'hit' and any lacking as a 'miss'. For pairs of sampling units there are therefore four possible outcomes – hit/hit, hit/miss, miss/hit and miss/miss. Probabilities of these outcomes can be estimated and compared with observed probabilities obtained by sampling. The full details of the method are presented by Pielou (1974).

Sampling points were marked out in Lower Ram Field at 73 points at 21 cm spacing on a lattice grid in March 1986. Concentric cores of 5, 10, 15 and 21 cm diameter were collected successively from each point with smaller cores forming part of the larger so that counts could be made for each core size at each sampling point..

Distances between each of the 73 points and every other point on the lattice were measured from a plan of the lattice creating more than 2000 values of a range of different lengths. Of these, six subsets were used corresponding to multiples of the distance between the sampling points (21 cm). The frequencies of hit/hit, hit/miss + miss/hit and miss/miss were calculated at these distances for each of the four core sizes.

Behavioural observations. Bibionid larvae are relatively inactive and slow moving so that real-time observations are impractical. A time-lapse video unit with a slow scan facility was used to record and track individual movements.

The larvae used in these studies (6th instar *B. johannis* and 4th instar *D. febrilis*) were collected from Lower Ram Field from December 1985 to February 1986. Larvae were kept in plastic petri dishes containing moist soil and turf at 12 °C with a L10:D14 photoperiod until required. All observations and video recordings were made with larvae in 8.5 cm plastic Petri dishes lined with moist filter paper.

The dishes and camera were enclosed in a cardboard cylinder above a diffuse, dim light source to reduce any directional, environmental stimuli. Heat generated by the light source was dissipated by inserting a water filled barrier between the light source and the dishes containing the larvae.

Preliminary observations were made by placing sixteen larvae 1 cm apart in a Petri dish so that, initially, no aggregations existed. Movement and behaviour were observed for at least two hours in an environmental chamber at 10 °C. Observations were replicated ten times.

Determination of aggregation. Tests were conducted at a temperature of 20 °C (±2) between 2.00 and 4.00 pm. Sixteen larvae were placed 1 cm apart as a 4 × 4 square in an 8.5 cm plastic Petri dish lined with moist filter paper. Larval positions were recorded at 5, 10, 15, 20, 25, 30, 40, 50 and 60 min post-introduction. Thirty replicate tests were undertaken for both *B. johannis* and *D. febrilis* larvae using fresh larvae each time.

An index of aggregation was calculated by adding the number of larvae not in contact with any other individual and the number of discrete aggregations consisting of two or more larvae. As a result, the index ranged from 1 (aggregation of 16 larvae) to 16 (no contact between larvae).

Role of tactile stimulation. Paired tests were run comparing the behaviour of a single larva and an inert object (either tightly rolled filter paper or a piece of cork cut to the same size as larvae) with that of two larvae. Only *B. johannis* larvae were used and both larvae and objects were placed in an 8.5 cm plastic Petri dish 2 cm apart on moist filter paper. Thirty replicates were run for two hours under time-lapse video observation during which time the number and duration of contacts were recorded.

Role of chemical stimulation. Ten *B. johannis* larvae were placed in a flat-bottomed glass tube on a 2 cm disc of moistened filter paper. After 24 h the contaminated disk was removed and placed in the centre of an 8.5 cm plastic Petri dish lined with moist filter paper. A single *B. johannis* larvae was placed on the disk and its movements recorded using time-lapse video. A control dish using an uncontaminated disk of filter paper was run in parallel. Thirty replicate pairs of 2 h duration were recorded and the number and duration of contacts with the disks noted.

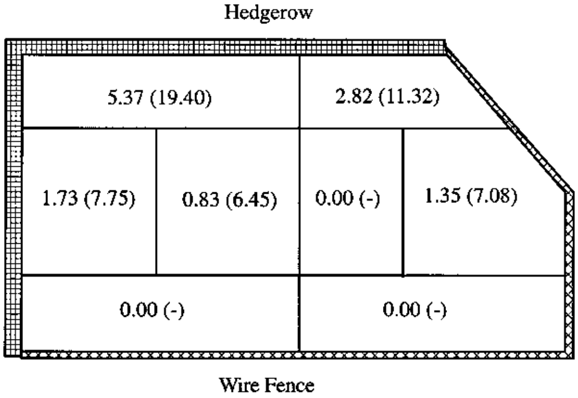

Figure 1. Sampled sub-sections of Lower Ram field and mean numbers of bibionid larvae recovered per core (standard deviation in parentheses).

Results

The bibionids recovered from soil sampling in these studies were all either *B. johannis* or *D. febrilis*.

Distribution between fields. Larvae (undifferentiated) were recovered from Newforge Lane (1.7% of cores; $\overline{x} = 0.53$; s.d. = 4.13), Baleyharvey Farm (6.7% of cores; $\overline{x} = 2.05$; s.d. = 11.45) and Hillsborough, Down (3.3% of cores; $\overline{x} = 0.78$; s.d. = 4.75). No larvae were recovered from Loughgall. At Ballyharvey Farm, bibionids were found in four out of the five fields that were sampled. The greatest number were recovered from Lower Ram field ($\overline{x} = 8.25$; s.d. = 32.13). Distribution within this field varied between sub-sections (Figure 1) with most being found along a hedge line. Mean populations of 1.53 (s.d. = 9.10), 1.00 (s.d. = 7.49) and 0.30 (s.d. = 2.32) were recovered from the remaining three fields.

Distribution along a hedgerow. The frequencies and mean numbers of larvae recovered for *B. johannis* and *D. febrilis* are shown in Table 1. Analysis of variance revealed significant differences in numbers of larvae between rows ($P < 0.001$), columns ($P < 0.001$) and sampling date ($P < 0.01$) but not between any of the interactions. Larval distribution tended to be localised with greater numbers 6–11 m from the hedgerow (Table 2).

Table 1. Recovery of bibionid larvae from soil samples ($n = 72$) collected alongside a hedgerow

	B. johannis			*D. febrilis*		
Sampling Date	Cores with larvae (%)	Mean count per core	Standard deviation	Cores with larvae (%)	Mean count per core	Standard deviation
9.11.84	5.6	4.04	25.16	0	0	–
23.11.84	15.3	2.90	10.53	0	0	–
7.12.84	9.7	1.40	5.06	1.4	2.32	19.68
21.12.84	15.3	2.65	9.45	4.2	2.42	19.22
4.01.85	15.3	1.33	7.64	4.2	1.00	5.85
1.02.85	29.2	4.43	11.47	8.3	5.46	21.42
15.02.85	25.0	4.92	26.74	2.8	0.49	2.93
1.03.85	29.2	3.93	10.53	5.6	1.68	10.78
8.03.85	29.2	2.13	4.37	5.6	3.80	24.89
15.03.85	33.3	1.74	3.29	5.6	0.24	1.31
22.03.85	22.2	1.64	4.48	6.9	0.35	1.80

Table 2. Cumulative numbers of Bibionid larvae recovered alongside a hedgerow

Distance from hedge (m)	*B. johannis*	*D. febrilis*
1	235	40
6	870	480
11	750	395
16	235	60
21	55	150
26	100	160

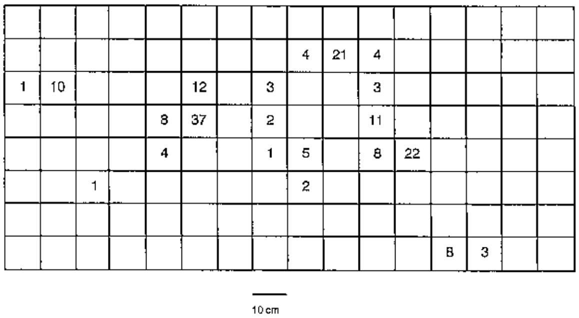

Figure 2. Numbers of *B. johannis* larvae recovered from congruent blocks of soil in a grass field.

Variance/mean relationship. The variance mean relationships for both *B. johannis* ($\log s^2 = 1.335 + 1.574 \log \overline{x}$; $r = 0.95$) and *D. febrilis* ($\log s^2 = 1.741 + 1.806\ log \overline{x}$; $r = 0.95$) showed that both species were highly aggregated for the size of soil core used.

Complete enumeration. The number of bibionid larvae (all *B. johannis*) recovered from each of the 128 blocks is shown in Figure 2. The extent of the aggregations was assessed by the systematic elimination of blocks from the data (starting with the block containing most larvae) so that the residual distribution could be tested for randomness (e.g. Usher, 1969). This process showed that the residual distribution gave a non-significant value for χ^2 (P $>$ 0.05 only after 17 of the 21 blocks containing larvae were removed. Almost all the larvae, therefore, were associated with aggregations so that there appeared to be 6–8 of these at distances of 20–40 cm apart.

The data were used to examine how estimates of distribution patterns change with increasing sample unit size using the mean-square method (Greig-Smith, 1983; Kershaw, 1964). Blocks were combined into samples of 2s, 4s, 8s, etc., and the mean square value calculated for each sample size. Thus for each sampling unit size, the number of individuals is counted, squared and summed prior to division by block size. A corrected sum of squares was calculated by subtracting this value from that of the next largest block size and the mean square obtained by dividing the corrected sum of squares by the degrees of freedom for the block size. Mean square values were plotted against block size (Figure 3) and showed peaks at 4 and 32 blocks. This suggested that there were at least two levels of aggregation between the sampling unit areas of 100 to 6400 cm^2.

Morisita's Index of Dispersion, $\mathbf{I}_\mathrm{d}$, (Morisita, 1970) was calculated for samples of different block sizes. For

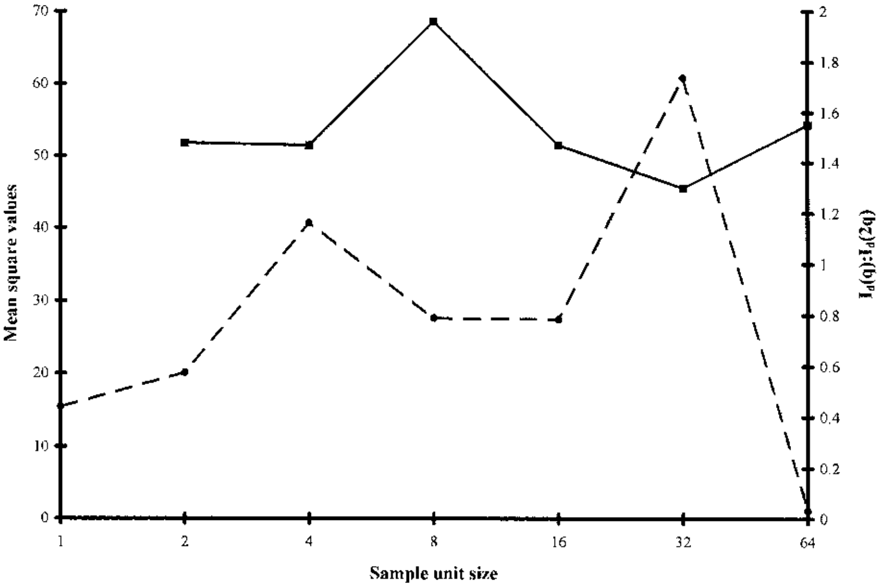

Figure 3. Mean square values (calculated according to Greig-Smith (1983) and Kershaw (1964) at differing block sizes and ratio of Morisita's index of dispersion $I_d(q)$ to $I_d(2q)$ at differing values of $2q$, where q is sample unit size. Calculated from data shown in Figure 2.

all except the largest sampling unit size (64 blocks) there were significant departures from randomness with $\mathbf{I}_\mathrm{d}$ values greater than one, indicating an aggregated distribution (Table 3).

Ratios of $\mathbf{I}_\mathrm{d}(q)$ to $\mathbf{I}_\mathrm{d}(2q)$ where q is a sampling unit size, were calculated and plotted against $2q$ (Figure 3). There was a peak at sample unit size 8 blocks, indicating aggregations occupying areas of 400–800 cm^2. There was an increase in the ratio value at the largest size suggesting a possible larger scale aggregation for areas in excess of 6400 cm^2.

Two-phase mosaics. Matrices of transition probabilities (Pielou, 1974) were calculated for the four different sized core samples (Table 4). These were then used to calculate expected frequencies of events for comparison with observed frequencies of hit/hit, hit/miss + miss/hit and miss/miss (Table 5). The total χ^2 values for the observed and expected frequencies increased with increasing core size. All four were significant ($P < 0.001$) and it was concluded that the patches and gaps of the sampled population did not form a random mosaic.

Behavioural observations. After 30–60 min, most larvae became part of a single aggregation. Larvae that became separated from aggregations displayed characteristic behaviour that involved swinging the whole anterior part of the body from side to side. On a number of occasions, usually after a period of more than 2 h, a second behaviour was observed when individuals became detached from aggregations. A gradual breakdown of the aggregation occurred with larvae closely following each other in a processional line. Gaps of up to 2 cm did not interfere with this process.

Determination of aggregation. The pattern of aggregation with time was similar for both species but *D. febrilis* achieved consistently lower mean index values (greater aggregation) than *B. johannis* (Table 6). For both species, the mean index value decreased more rapidly during the first 30 min of observation than it did in the second.

Role of tactile stimulation. Significantly more contacts ($P < 0.001$) were made between the two larvae ($\overline{x} = 3.33$, s.d. $= 1.97$) in the control dishes than between the single larva and inert object ($\overline{x} = 1.73$, s.d. $= 1.62$) in the test dishes. The total contact duration in the control ($\overline{x} = 2269$ s, s.d. $= 1545$) was also greater ($P < 0.001$) than that of the test ($\overline{x} = 1188$ s, s.d. $= 1343$). Moreover, the frequency of contacts (i.e. the total non-contact time divided by the total number of contacts) was greater in the control than in the test dishes ($P < 0.001$).

Table 3. Morista's Index of Dispersion ($\mathbf{I}_d$) for different sizes of sampling unit

Blocks per sample	Number of samples	mean (m)	variance (s^2)	$\mathbf{I}_d$	χ^{2*}
128	1	170	–	–	–
64	2	85	72	0.99	0.9^a
32	4	42.5	1309.7	1.53	92.5^b
16	8	21.3	531.1	1.99	174.9^b
8	16	10.6	241.7	2.93	341.4^b
4	32	5.3	142.5	5.74	831.7^b
2	64	2.7	55.5	8.42	1314.2^b
1	128	1.3	21.6	12.44	2057.4^b

$^{*}\ \chi^2 = \frac{s^2}{m}\,(n-1)$ d.f.
Probability of a significant departure from randomness;
a = $P > 0.1$ $(n - 1)$ d.f.; b = $P < 0.001$ $(n - 1)$ d.f.

Table 4. Transition probabilities for sampling with paired sampling units of four different diameters: H, hit; M, miss

Sampling unit diameter (cm)	Matrix of transition probabilities, P*	
5	0.638	0.362
	0.017	0.983
10	0.710	0.290
	0.030	0.970
15	0.698	0.302
	0.041	0.959
21	0.692	0.308
	0.054	0.946

$$^{*}\ P = \begin{array}{llcc} & & \text{Second sampling unit} & \\ & & \mathbf{H} & \mathbf{M} \\ \text{First sampling unit} & \mathbf{H} & P^{1,1} & P^{1,2} \\ & \mathbf{M} & P^{2,1} & P^{2,2} \end{array}$$

Role of chemical stimulation. Paired t-tests showed that there was no significant difference ($P > 0.05$) in the number of contacts made between larvae and the contaminated test ($\overline{x} = 1.33$, s.d. $= 1.12$) and control disks ($\overline{x} = 1.50$, s.d. $= 0.73$). However, the duration of larval contacts with test disks ($\overline{x} = 5204$, s.d. $= 2777$) was significantly greater ($P < 0.001$) than with control disks ($\overline{x} = 2265$ s, s.d. $= 2490$). By implication, the frequency of contacts with the test disk was greater since more time spent in contact with a disk left less time for further contacts to be made.

Discussion

This study has shown that bibionid larvae are found in agricultural swards in Northern Ireland but that their occurrence is sporadic and numbers are variable. This pattern is not confined to different areas within the region but repeats itself at farm, field and within field scales. Hedgerows are important features of the landscape in Northern Ireland and the results from these studies shows that they are an important factor in determining the spatial distribution of bibionid larvae.

Table 5. Observed and expected frequencies of bibionid occurrence in sampling unit pairs at six distances apart

		Core size (cm)							
		5		10		15		21	
Distance (cm)	Event	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
	H/H	1	5.3	6	12.4	7	15.6	10	19.3
21	H/M	24	6.1	44	10.2	57	13.5	70	17.2
	M/M	162	175.6	137	164.4	123	157.8	107	150.5
χ^2		57.1^{c}		119.9^{c}		152.6^{c}		179.2^{c}	
	H/H	0	2.8	4	7.4	5	9.2	6	11.4
42	H/M	22	8.1	42	14.1	53	18.4	65	23.2
	M/M	132	143.1	108	132.5	96	126.4	83	119.4
χ^2		12.2^{b}		61.3^{c}		74.3^{c}		89.0^{c}	
	H/H	0	1.5	2	4.6	4	5.6	5	6.9
63	H/M	17	8.2	37	15.1	45	19.0	53	23.7
	M/M	109	116.3	87	110.2	77	101.4	68	95.4
χ^2		6.0		43.4^{c}		41.9^{c}		44.6^{c}	
	H/H	0	0.8	3	2.6	3	3.3	7	4.2
84	H/M	14	7.1	25	13.1	34	13.1	34	20.7
	M/M	84	90.0	70	82.3	61	55.9	57	73.1
χ^2		5.1		11.5^{b}		17.9^{c}		14.0^{c}	
	H/H	1	0.4	1	1.5	3	1.9	6	2.5
105	H/M	8	5.5	20	10.3	21	13.1	23	16.1
	M/M	62	65.1	50	59.2	47	55.9	42	52.4
χ^2		1.8		8.6^{a}		6.8^{a}		7.9^{a}	
	H/H	0	0.2	1	0.9	1	1.2	4	1.6
126	H/M	7	4.3	13	8.1	15	10.3	17	12.5
	M/M	46	48.5	39	44.0	37	41.5	32	38.8
χ^2		1.5		3.4		2.3		4.6	
Total χ^2		83.7^{c}		248.1^{c}		295.8^{c}		339.3^{c}	

a $= P < 0.05$; b $= P < 0.001$; c $= P < 0.001$.
H = Hit (bibionids found); M = Miss (bibionids not found).

Swarming is a typical feature of reproductive behaviour for the males of most Bibionidae which form loose but extensive swarms over grassland. Females are much less active and are usually found resting on vegetation close to the ground or feeding at flowers. In warm weather, swarming begins directly after emergence and the short teneral period. It occurs over, or close to, the emergence site and swarms often form around ‘markers’ such as overhanging branches, elevated objects or free-standing bushes in open grassland (Zeil, 1983). Hedges and hedge trees may act as markers in this way.

It has been shown (Lewis, 1969) that, even on the windward side, sheltered zones of reduced wind activity can occur at a horizontal distance of up to twice the height of a hedge. Since the average height of the hedge in this study was approximately 5 m, the expected shelter would extend about 10 m out. This is consistent with an influence on female post-mating flight that results in peak numbers of larvae in an area 6–11 m from the hedge.

Table 6. Changing aggregation index over time for larvae of *B. johannis* and *D. febrilis* ($n = 30$)

	B. johannis		*D. febrilis*	
Time interval (min)	Mean	Standard deviation	Mean	Standard deviation
1	15.90	0.30	15.80	0.48
5	13.90	0.64	10.40	0.84
10	11.80	0.76	9.33	0.70
15	10.20	0.54	7.70	0.86
20	9.13	0.62	6.23	0.76
25	8.23	0.67	5.13	0.62
30	6.30	0.86	4.13	0.50
40	5.37	0.60	3.83	0.58
50	4.77	0.56	3.20	0.60
60	4.90	0.60	3.50	0.96

Bibionid larvae are not confined to field margins adjacent to hedgerows. Results from Lower Ram field show that they will be found in the middle of fields, albeit at lower numbers. The presence of an electricity pole in the centre of this field may have acted as a marker for swarming.

Each of the methods used to assess the spatial distribution of bibionid larvae in this paper determined that they were highly aggregated in grassland. Use of different spatial scales did not alter this so it can be concluded that aggregation is an aspect of the biology of bibionids rather than an artefact of the experimental method.

Dilophus febrilis showed evidence of greater aggregation than *B. johannis* in the laboratory studies with a consistently lower aggregation index over time. This was also reflected by the slopes of the log variance/log mean relationships derived from field samples and therefore represents a quantitative difference in the biology of the two species. The reason for this is unknown.

Two levels of aggregation were apparent. The first consisted of intimate groups of larvae occupying 400–800 cm^2 with gaps of 20–40 cm between them. These larval clumps were not, however, randomly distributed and showed evidence of aggregation at a larger scale.

Female flies will search for oviposition sites and select them on the basis of their suitability as sources of food (eg Vorsatz & Rode, 1967) and environmental requirements for larvae. The primary level of aggregation probably results from a micro-distribution of individuals arising from a single female. There is now sufficient evidence to suggest that these primary aggregations are maintained by a chemical attraction between individuals. They are not only able to remain clustered but can follow trails so that the integrity of the group is not lost by individuals becoming detached. The spacing between clusters may simply reflect the distribution of food sources or could also be due to mechanisms whereby gravid bibionid flies avoid already occupied patches.

The secondary, or larger scale, aggregations will be due to factors influencing the distribution of adults. Shelter and the distribution of swarming markers are important and mating takes place in areas favouring adult flight. Selection of oviposition sites will occur within these zones. The aggregated nature of bibionid larvae at various spatial scales shown in the study is the outcome from larval behavioural responses and environmental influences on the adult female in her choice of oviposition site.

Bibionids of agricultural interest tend to be grassland insects and most damage to crops has occurred after grassland has been ploughed (D'Arcy-Burt & Blackshaw, 1991). They are sufficiently sporadic as pests to warrant monitoring but their highly aggregated distribution will make whole field assessments too expensive. The importance of hedgerows in determining in-field larval distribution is established and, coupled with knowledge of the role or organic manures in promoting numbers (D'Arcy-Burt & Blackshaw, 1991), suggest a strategy of initial monitoring at those boundaries, especially if slurry has been applied to a sward. If larvae are not numerous in these areas then damaging populations across the field are unlikely.

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