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Studies on selected aspects of the ecology of *Velia caprai* and some *Gerris* species.

by

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Submitted as part of the requirements for the M.Sc. Degree,
University of Durham, September 1971.

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Introduction

The genera Velia Latreille and Gerris Fabricius belong to the series Amphibicorisae, the surface-dwelling water bugs. They are specialised for a predatory life; eyesight is well developed, the short front legs are adapted for grasping prey, and the bugs support themselves on the tips of the middle and hind legs which in Gerris are very thin and elongate.

They feed mainly on terrestrial insects which fall onto the water surface. (Curtis Riley 1918). Feeding does not occur when it is raining, the bugs take shelter in nearby vegetation. Most active feeding occurs during fine weather with a moderate wind to bring in food. (Lumsden 1949).

Until 1951 it was thought that all British Velia belonged to the species V. currens Fabricius, but Brown (1951) showed that there are two species in this country, neither of them V. currens. V. caprai Tamanini is the species investigated here; V. saulii Tamanini is much less common than V. caprai (Macan 1965). There are 9 species of Gerris in this country, of which the following were found during the present study: G. lacustris (Linnaeus), G. odontogaster (Zetterstedt), G. lateralis (Schummel), G. thoracicus (Schummel), and G. costai (Herrich-Schaeffer). All adults were identified according to the Freshwater Biological Association Scientific Publication No.16, Revised Key to the British Water Bugs (Hemiptera-Heteroptera) by T. T. Macan, 1965. There is no key to the identification of Gerris nymphs of the first three instars; Brinkhurst (1959b) gives a key to the identification of fourth and

fifth instar nymphs, but this was found to be unsuitable for live nymphs in the field.

The habitats of V. caprai include streams, peat cuttings and ponds with a slight flow, usually where there is a low amount of organic matter in solution, (Brown 1954; Walton 1943), and overhanging vegetation (Popham 1945). V. saulii prefers larger water bodies than V. caprai, being found on the margins of lakes and rivers, chiefly in the northern half of Britain (Brown 1954). V. caprai is found in most parts of Britain.

G. lacustris, also found in most parts of Britain, tolerates a lower surface tension than most other Gerris species and is often found on ponds with a high organic matter content, (Walton 1943). It is common on pools, ponds and lakes, but also occurs on mere marginal habitats with all other Gerris species, often in mixed population. (Brinkhurst 1959a).

G. odontogaster, which is probably present throughout Britain, is an inhabitant of weedy ponds, canals, lakesides and various acid waters, living close to the shore. The habitats of this and G. lacustris are difficult to distinguish (Brinkhurst 1959a). These two species frequently occur in mixed populations. Brinkhurst records that on one pond where both species were present, G. odontogaster occurred all round the shores, and the only G. lacustris found were limited to a small area beneath a large oak tree.

G. lateralis is boreo-alpine in distribution, having greater abundance in northern Britain. It inhabits still or stagnant water in ditches, peat holes or pools, often with dense vegetation (Pearce and Walton 1939, Brown 1948).

It has been taken with G. costai (Brinkhurst 1959a).

G. costai is an upland species confined to peat pools and stream margins, mostly restricted to northern Britain, (Brown 1948, Walton 1943).

G. thoracicus has a mainly coastal distribution, being tolerant of brackish water (Lindberg 1949). It occurs in small numbers inland often during the post-overwintering distributive phase in April-May. (Brinkhurst 1959a).

All species of Velia and Gerris hibernate during the winter, and there is high mortality during this time (Brinkhurst 1966). The macropterous forms often fly far from water to hibernate, though apterous forms overwinter near the water. (Brinkhurst 1958). Flight occurs chiefly in autumn and spring, prior to and after hibernation. All species of Gerris and Velia mate and lay eggs in spring, and some species lay a second batch of eggs in mid-summer. There are five nymphal instars which give rise to adults in summer, which then overwinter and lay eggs the following spring. (Southwood and Leston 1959).

In recent years much interest has been focused on wing polymorphism in the Gerroidea. Many authors have put forward possible explanations for the wide range of alary polymorphs and the ratios between these in different generations. (Ekblom 1941-1950, Förster 1954, Jordan 1943, and 1947, Brinkhurst 1958). The most recent work shows that wing polymorphism is controlled by the action of low temperature upon a genetic switch mechanism at the time of vitellogenesis (Brinkhurst 1963).

Much information has been gained about the ecology of these bugs both from experimental work on reactions to factors such as lowering of surface tension, and varying

wind and water speeds, and also general observations by many authors on habitat and distribution. The aim of the present study was to investigate some of the differences in ecology portrayed by the various species in mixed populations in the field; to examine any correlation with size of pond, vegetation pattern, potential food, egg-laying pattern, and movement into and out of ponds, and for Velia movement up and downstream.

Description of Study Areas.

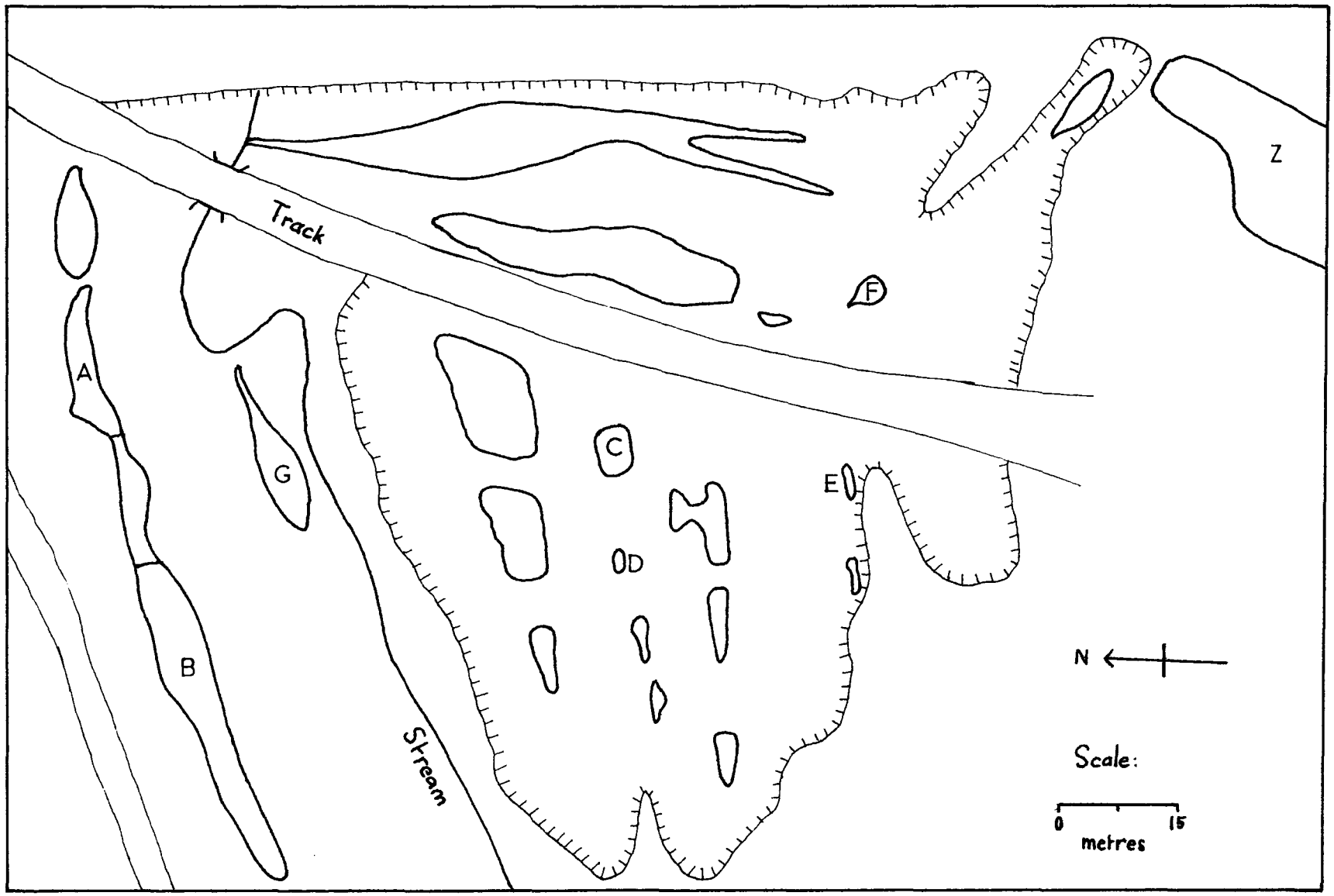
The fieldwork was carried out on three sites, which will be referred to as Brasside, Moorhouse and the Durham Field Station; the first two being the main study areas and the latter was used for one experiment on the movement of V. caprai, and as an additional source for specimens of G. lateralis and G. lacustris for the egg-laying study.

1) Brasside ponds. (see fig. 1)

(National Grid Ref. NZ 45/290452; height 200' (60.96m) O.D.)

These ponds were situated in an area of 2-3 acres (0.8-1.2 hectares) near to the village of Brasside, Co. Durham. The locality is 2 miles (3.2 km) to the north-east of Durham City; and lies on laminated clays which at this point are 70 feet (21.3 m) thick (Maling 1955). The ponds have formed in old clay workings abandoned in the 1930's, and now support a very rich and varied flora and fauna. (Morphy 1966). The area contains about 20 ponds of varying sizes many of which are ill-defined and merge into the surrounding marshy ground. Most of the ponds lie in a depression about 8-10 feet (2.4-3.0m) below the level of the surrounding ground, and thus form an artificial

FIGURE 1. Sketch-map of the ponds at Brasside.


Track
A
B
C
D
E
F
G
Z
Stream
N
Scale:
0
15
metres

drainage system. The water level is maintained by rainfall and seepage from the surrounding clay; small temporary outlets are formed from some ponds after heavy rainfall. Pond Z is on a similar level to the surrounding land. Ground adjacent to the ponds is used as rough grazing (chiefly Nardus stricta) for cattle. There are a few scattered bushes of hawthorn (Crataegus monogyna), dog rose (Rosa canina), willow (Salix sp.), bramble (Rubus sp.) and isolated groups of oak trees (Quercus sp.)

Other water bodies in the vicinity include three small lakes, each 2-3 acres (0.8-1.2 hectares) in area. These are also abandoned clay workings.

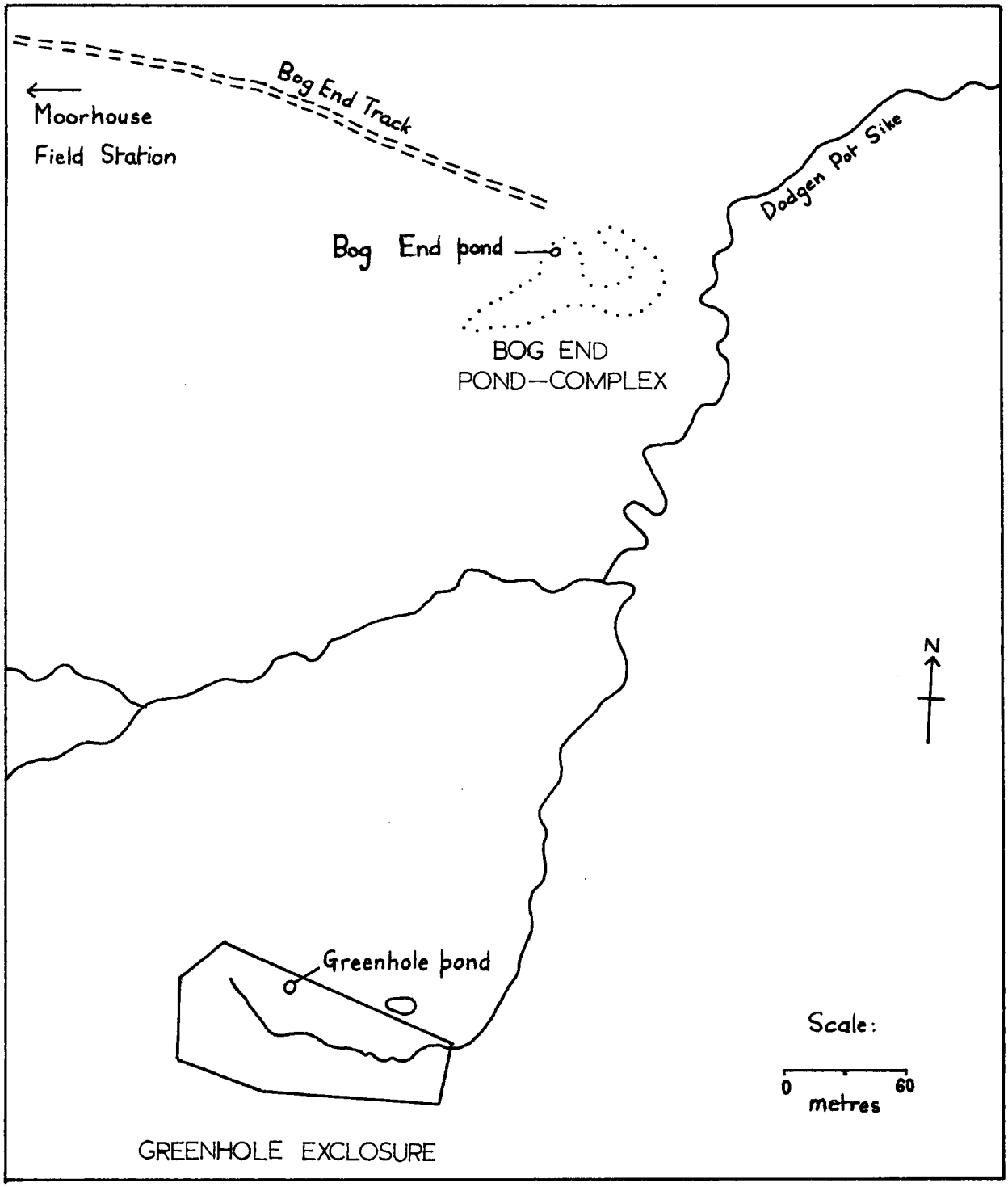
Durham receives an average of 25 inches (63 cm.) of rain annually, and has an average summer temperature of about 14°C. The Brasside ponds are in a fairly exposed position, and are affected by winds from all directions.

Various workers have studied different groups of animals at Brasside, though no previous work has been done on Gerris species.

2) Moorhouse.

Moorhouse National Nature Reserve (N.R.80) is situated in the Pennines in Westmorland, and its climate has been described by Manley (1942) as sub-arctic. It receives a precipitation of 70"-80" (180-200 cm.) annually, 15% of which falls as snow. The relative humidity is rarely less than 60%. The average summer air temperature is a little more than 10°C, and temperatures below freezing occur during nine months of the year. (Brown, Cragg and Crisp 1964). The Reserve consists of mixed moor with no native trees, the only shelter being given by the low hills,

FIGURE 2. Sketch-map of area containing study-ponds, Moorhouse.


Bog End Track
Moorhouse
Field Station
Dodgen Pot Sike
Bog End pond
BOG END
POND—COMPLEX
N
Greenhole pond
Scale:
0
60
metres
GREENHOLE EXCLOSURE

rounded by past glacial action and much dissected by numerous streams. Most of the area is covered with a layer of peat of varying depth up to 7 feet (2m.).

Work on different groups of invertebrates has been carried out by many authors, though no extensive study has previously been made of Gerris and Velia on the Reserve.

In a general investigation of invertebrates on the Reserve, Nelson (1971) records that G. costai and Velia caprai were present in peat pools. G. lateralis, the other speciesfound during the present study on the Reserve, was not recorded. Nelson comments on the extreme paucity in the variety of fauna at Moorhouse, and also the reluctance of some commoner insect species to fly.

Heal (1963) lists the location, size and chemical status of many of the ponds on the Reserve. Most of those within reasonable distance of the Moorhouse Field Station were visited before ponds were selected for study. Eventually two suitable ponds were found, one at Greenhole, (Nat. Grid Ref. NY 764324; 1900 feet (570 m.) O.D.) and the other at nearby Bog End (Nat. Grid Ref. NY 765328, 1870 feet (560 m.) O.D.) (See fig. 2).

Greenhole is an enclosure situated in a narrow valley running NW to SE. A stream, Dodgen Pot Sike, rises in the south-east corner. In the centre of the enclosure limestone of the Tynebottom limestone series is exposed, and the associated soil is fertile, supporting typical limestone grassland. On other parts of the enclosure redistributed peat supports Calluna, Sphagnum and Juncus squarrosus, and a few Pinus sylvestris have been planted. The pond is situated in a sheltered hollow on the south-facing slope; this slope sometimes became very warm in summer sunshine.

The depression which now forms the pond was probably man-made, since there are abandoned mines nearby. Although situated on peat, the pond is about 5 feet (1½ m.) deep and is probably enriched chemically by the underlying limestone.

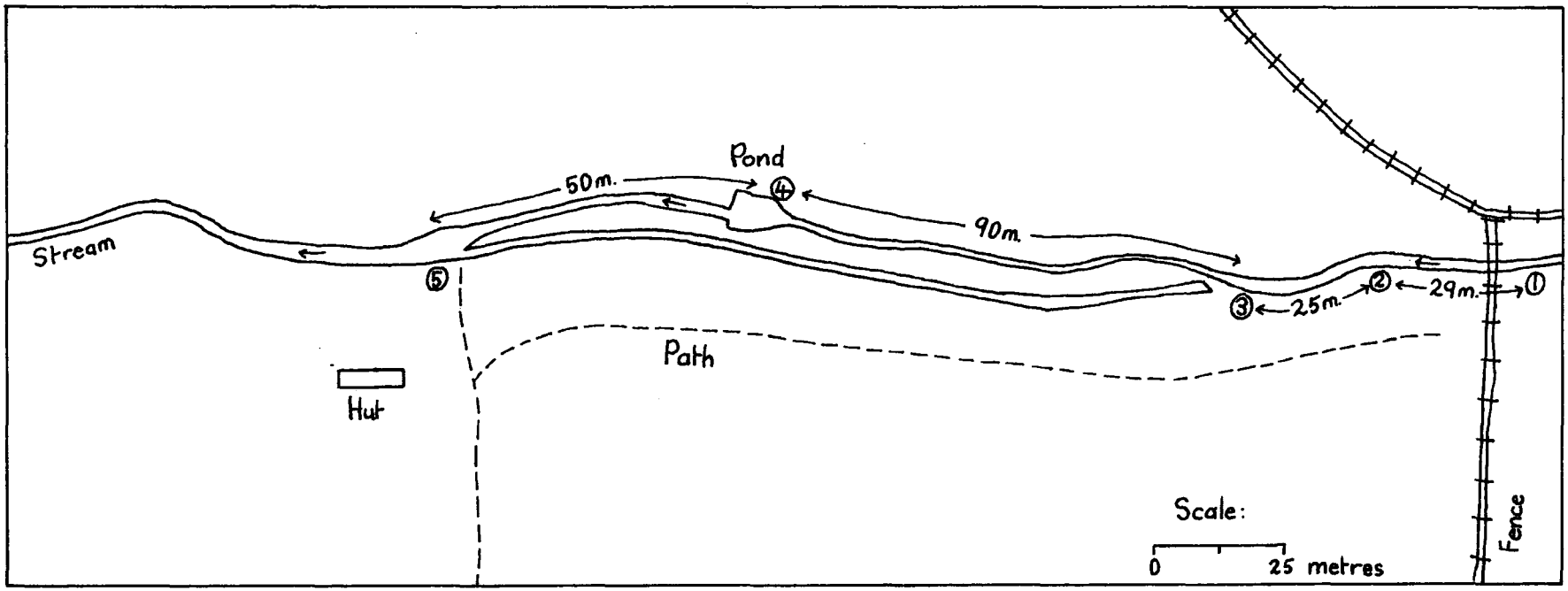
Bog End is situated about 1/4 mile (380 m.) from Greenhole, and includes a number of peat pools and streams among abandoned mine-workings. Many of these are choked with Juncus conglomeratus, Equisetum and Carex. None of the ponds are more than a foot (30 cm.) deep, though the water level fluctuates considerably with rainfall.

Greenhole supports a population of G. costai, and Bog End population of G. costai and G. lateralis. Of the other ponds visited, those at Nether Hearth (Nat. Grid Ref. 762 330) support G. costai, and another group of ponds (Nat. Grid Ref. 758 328) G. costai and G. lateralis. Velia caprai were seen in several streams and peat ponds including Bog End, sometimes where Gerris species were also present.

3) Durham Field Station.
(Nat. Grid Ref. NZ 274406; 250 feet (75 m.) O.D.)

This area is managed by the Zoology Department of Durham University, and occupies 9.5 acres (3.8 hectares) on both sides of a small valley. A stream, which has a maximum width of 5 feet (1.5 metres), runs south through the reserve. It is a small tributary of the River Wear, which it joins 3/4 mile (1200 m.) south of the Field Station. The stream has been diverted at the top of the reserve to form two small ponds behind dams. (see fig. 3). The lower one is covered by wire mesh and is being used by

FIGURE 3. Sketch-map of Durham Field Station, showing sites at which *Velia caprai* were sampled.


Pond
50m.
④
90m.
Stream
⑤
③
25m.
②
29m.
①
Path
Hut
Scale:
0
25 metres
Fence

another worker.

The valley, situated in a small bowl of high ground, is southerly in aspect and generally fairly sheltered from wind; otherwise it has similar climate to that of Brasside. The soil type is brown earth overlying coal measures. The eastern side of the valley is a fairly steep wooded slope, the canopy consisting chiefly of oak (Quercus robur) and beech (Fagus sylvatica). There are trees at intervals along most of the stream bank on this side; apart from these the dominant vegetation along both sides of the stream is Dactylis glomerata (cocksfoot), Lolium perenne (rye grass) and Juncus effusus.

The stream supports a large population of Velia caprai, concentrated at particular points along its length. The upper pond contained Velia caprai, G. lacustris, a few G. lateralis, and one specimen of Gerris najas was observed.

Introduction to Marking Methods.

Brinkhurst (1956), in his study of population dynamics and migration of Gerris najas on Lake Windermere, marked the individuals with nail varnish. They showed some irritation for a few minutes, turning over on their backs and making cleaning movements as though in an attempt to remove the marks, but did not suffer permanent harm. Brinkhurst, using this method of marking, demonstrated migration between boathouses, and also that some of the individuals marked in autumn reappear in the same boat-house in spring. He found that nymphs could not be marked in this way, the marks either killed them or prevented ecdysis; also since nymphs are very delicate, any handling is likely to damage them.

Southwood (1968) discusses marking methods in general. He emphasises that marks should not make the insect more conspicuous to predators, and should not be such that they are removed by the cleaning movements of the insect. He suggests various dyes and paints for use in marking, and methods of handling the insects.

The method of marking decided upon for this experiment was aerosol cans of nitrocellulose paint. These have the advantage that small quantities can be sprayed onto the lid, and then can be applied to the insect before the paint dries, and once on the insect it dries quickly. Various tools for applying the paint, such as single hairs and entomological pins, (as suggested by Southwood) were tried, but the best tool was found to be a fresh blade of Juncus effusus (which grew on all the study areas). All the suggested methods of handling were found unsuitable; the best way was to gently hold the bug by two or more legs between finger and thumb while marking.

Practice in marking was obtained first on Velia caprai as these were easier to obtain in large numbers than Gerris. Only the femurs of the middle and hind legs, and also the thorax were suitable for marking in this way on Velia. Gerris were less active while being marked and generally easier to handle. Since the femurs of Gerris are considerably more elongate than those of Velia, there was room for two marking positions on the femur proximal and distal to the body. Again only the middle and hind legs, and thorax were suitable for marking. The fore legs were never marked, since these are used for feeding and cleaning the sense organs. On both Gerris and Velia it was essential to avoid getting paint on the joints of the legs. When

the paint was applied thinly to the right places, it dried within a few seconds and could not be removed by the insects. When all these precautions were observed, both Velia and Gerris survived as well when marked as unmarked, and the marks did not come off.

With the eight different marking positions on the legs alone, and various combinations of these, a total of 255 individual patterns was theoretically possible. In practice no insect was marked in more than four positions and for ease in recording different colours were used when the simplest patterns had been exhausted. A total of five colours increased the possible patterns to 959,615; though only a few hundred of these were used.

Three experiments were carried out using this marking system:-

1) Distribution of Velia caprai on a small stream.

2) Marking of individual gerrids on selected ponds to determine dispersal, births and deaths.

3) Estimation of total numbers of gerrids and movements between opposite sides of ponds.

INDIVIDUAL MARKING EXPERIMENT.

Aims and description of ponds.

Adult gerrids were marked so that they could be individually distinguished, in order to record their movements into and out of ponds, births and deaths, and the total numbers present on different dates over an extended period.

Four ponds were selected for this experiment, two at Brasside and two at Moorhouse. Since the intention was that all adults should be captured at each visit, the ponds had to be small, yet with a reasonable population density of gerrids; all parts of the pond had to be within reach of a pond net; and also each pond should not be connected by any clear water surface to other ponds. Where this latter restriction was not adhered to, the connecting channels were sealed. Ponds of differing vegetation pattern were chosen in each place, though these patterns changed considerably during the period of study.

Pond E at Brasside (see Fig.10) was 18 feet (5.4m.) long with a maximum width of 6 feet (1.8m.). The vegetation around the edges consisted of Eleocharis, Equisetum, and Juncus effusus; there was no floating vegetation. All the vegetation grew considerably during the period of study, and by the end of it the narrow part of the pond was completely shaded by Juncus effusus. Around the wider part of the pond the vegetation became severely trampled by cattle, so that the vegetation bent over into the water leaving an area of surface only a quarter what it was at the beginning. The surrounding area was marshy, and the nearest ponds

were about 20 feet (6m.) away; there were a total of some 50 ponds of varying sizes all within half a mile (800 m.) of pond E.

Pond F at Brasside was 16 feet (4.8m.) long with a maximum width of 11 feet (3.3m.). The vegetation around the edges was Equisetum, Eleocharis, and Juncus effusus; the latter grew into the water for about 3 feet (90 cm.) at each end of the pond. At the beginning of the experiment the only vegetation in the middle of the pond was Potamogeton natans very sparsely distributed. Later, Lemna trisulca and Equisetum grew up, though the density of all these was still low.

Greenhole pond at Moorhouse was circular, 10 feet (3 m.) in diameter, but three quarters of the area was covered with Sphagnum, leaving a half-moon of open water surface about 10 feet (3 m.) long by 4 feet (1.2m.) wide at the beginning of the experiment. During dry periods towards the end this area of open water was almost totally taken up with the Sphagnum which had previously been submerged. The surrounding vegetation was Calluna, Sphagnum, and a few young Pinus sylvestris. The nearest pond to this was 30 feet (9m.) away on the other side of a bank which stood 6 feet (1.8m.) above the pond and was covered with Calluna and Pinus sylvestris. The other pond was 40 feet (12m.) long by 30 feet (9m.) wide and had populations of G. costai and G. lateralis. The next nearest ponds to Greenhole pond were about a quarter of a mile away at Bog End. (See Fig.21).

Bog End pond at Moorhouse was circular, and 8 feet (2.4m.) in diameter. The surrounding vegetation was Juncus conglomeratus, and Equisetum. During the period

of study most of the surface became covered with Equisetum and Potamogeton natans. The water level was very variable; in times of flood water probably flowed from an outlet (see Fig.14). The surrounding area was marshy, with about six other small ponds and water channels.

Methods.

The ponds were visited weekly whenever possible, on each occasion all the visible adults were captured, using a pondnet. A minimum time of three quarters of an hour was spent on each of the three larger ponds, and on all ponds hunting was continued as long as adults were being observed. When captured they were placed in a white enamel dish and covered with a sheet of perspex to prevent them flying away. For those individuals already marked, their marks were recorded; the unmarked ones were given new individual marks which were also recorded, then all were returned to the pond.

Results

The tables showing individual captures on the ponds on successive dates are given in appendices 1-4. From these, the numbers of gerrids gained and lost from the ponds on successive dates were calculated. (See Table 1.)

Analysis of Results.

a) Proportions caught. (See Appendices 1-4).

These figures are affected by a number of factors. Their reliability depends on both the magnitude of the catch and the number of catches before and after the date, to determine the true proportions caught. It would seem likely that an increase in vegetational cover would reduce the proportion caught; conclusions on this are given below for the individual ponds. In general, the 'proportions caught' for different species seem to vary consistently with the date; this suggests that weather also plays an important role in determining the proportions caught, rain being the main factor lowering catching success.

On pond E the figures were too low to say whether there was a difference in proportions caught for the different species. The total proportion caught shows no overall trend during the season. It would be expected that the reduction of clear water surface due to trampling of the vegetation would reduce the proportion caught later in the season, but there is no clear indication of this. The proportions caught were generally high except for 18 June when it was raining.

TABLE 1. Numbers of gerrids gained and lost from the ponds on successive dates.

POND E.

Species	Dates 25/5		31/5		10/6		18/6		27/6		12/7		19/7		29/7		30/7		5/8		Total	
	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
G. odontogaster	1	0	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	4
G. lacustris	1	1	3	0	0	6	0	3	0	0	0	2	0	0	0	0	1	0	2	0	7	12
G. thoracicus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
G. lateralis	1	0	1	0	0	1	0	0	0	0	0	1	0	0	2	0	0	2	0	0	4	4
Total gained	3		4		0		0		0		0		0		2		1		2		12	
Total lost	1		2		9		4		0		3		0		0		2		0		21	

POND F.

	3/5		12/5		18/5		25/5		1/6		9/6		18/6		24/6		12/7		19/7		29/7		5/8		Total	
	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
G. odontogaster	2	0	3	0	2	0	1	1	1	2	0	3	0	1	2	1	0	6	0	0	6	0	7	0	24	14
G. lacustris	1	1	5	0	2	0	0	2	2	1	0	2	0	4	0	3	0	0	0	0	0	0	0	0	10	13
G. thoracicus	0	0	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
G. lateralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1
Total gained	3		10		4		1		3		0		0		2		0		0		7		7		37	
Total lost	1		0		1		3		4		5		5		4		6		0		0		1		30	

TABLE 1. (2)

BOG END POND

	Dates 17/5		26/5		2/6		8/6		25/6		1/7		8/7		13/7		20/7		28/7		3/8		Total	
	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
G. costai	1	1	0	0	1	0	0	0	0	2	0	2	0	0	0	0	0	0	0	1	0	0	2	6
G. lateralis	0	0	4	1	4	4	0	2	0	6	1	3	0	0	0	3	0	0	0	0	5	2	14	21
Total gained	1		4		5		0		0		1		0		0		0		0		5		16	
Total lost	1		1		4		2		8		5		0		3		0		1		2		27	

GREENHOLE POND

	29/4		5/5		11/5		17/5		26/5		2/6		8/6		25/6		1/7		8/7		13/7		20/7		28/7		3/8		Total	
	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
G. costai	0	1	0	6	1	0	1	3	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	16
Total gained	0		0		1		1		0		0		0		0		0		0		0		0		0		0		2	
Total lost	1		6		0		3		6		0		0		0		0		0		0		0		0		0		16	

\+ number gained − number lost.

Pond F similarly shows no overall decrease in proportion caught, and the low figures can be correlated with rain, the proportions caught on fine days were quite high.

On the Greenhole pond the proportion caught was consistently high, confirming that the gerrids were very easily visible. On the only day (29 April) when one was missed, it was raining.

At the Bog End pond there is some indication that the proportion caught was lower later in the season when the vegetation had grown up markedly. The proportions caught are more variable than for the Brasside ponds. The low figures can be correlated with rain. Lumsden (1949) records that during rainstorms, no G. najas were observed on an open surface of water where they were abundant in fine weather.

b) Total numbers caught on different dates. (See appendices 1-4).

For ponds E, F and Bog End pond there is a pattern of moderate numbers (at the start of the study) building up to a peak, then falling away to a minimum, then rising again at the end of the study.

Table 2. Dates when maximum and minimum numbers of gerrids occurred on the ponds.

Pond	First maximum	Minimum	Second maximum started.
E	31 May	12 - 19 July	19 July
F	18 May	12 - 19 July	19 July
Bog End	2 June	28 July	28 July

Since records were not kept of pond E until 21 May, it is possible that numbers were higher before this date, corresponding to the maximum on pond F on 18 May. The maximum at Brasside

seems to have been earlier than at Moorhouse, though the data are not sufficient to say exactly how much earlier.

Ponds E and F have their minimum (no individuals) between 12 July and 19 July. This was a very dry period and both ponds had very low water. Again the minimum at Bog End (3 individuals) occurs about a fortnight later than at Brasside. Since the second maximum did not occur during the period of the experiment, only the dates when a steady increase started can be compared. Again the increase started nine days earlier at Brasside than at Moorhouse.

Hence the cycle of population numbers for Moorhouse was approximately a fortnight behind that at Brasside, though the ponds were not visited at sufficiently frequent intervals to quantify this difference accurately.

The pond at Greenhole did not fit into this cycle, having its maximum (14 individuals) on the first date of the experiment, and falling to a minimum (no individuals) on 26 May, much earlier than any of the other ponds. The second increase did not occur during the experiment, though nymphs were observed from 2 June onwards, and on the 3 August only one late instar nymph was observed. The possible reasons for this are discussed below.

Numbers gained and lost (see Table 1.)

The peaks in gains and losses occur about a fortnight later at Moorhouse than at Brasside. Greenhole seems to follow a different pattern from the other ponds, the reasons for this are discussed below.

TABLE 3. Peaks in gains and losses on the ponds.

Pond	First peak in gains.	Second peak in gains.	Main losses
E	31 May	29 July onwards	10 June
F	12 May	29 July onwards	9 June
Bog End	2 June	2 August onwards	25 June - 1 Jul
Greenhole	11 May	-	5 May, 26 May

It is likely that if records had been kept for pond E from the same time as pond F, pond E would also have had its first peak in gains on 12 May.

Table 3 points to the need to consider the causes of gains and losses. Which of the gains were due to immigrations and which to appearance of new adults, and which of the losses were due to deaths and which to emigrations?

Since no new adults were recorded on any ponds at Brasside before 7 July, and at Moorhouse before 28 July, all gains up to this time must be due to immigration, either by flight, or in the case of wingless individuals by walking from overwintering sites. Gains after this time were probably all due to the appearance of new adults, since the chief period of flight in gerrids is April - May (Brinkhurst 1958). While immigration is occurring it seems likely that emigration is also occurring. The total number of gains up to 1 July was 60, while the total number of losses was 102. (See Table 4). Whereas for the gains it is clear which of these is due to immigration and which to the appearance of new adults, it is more difficult to distinguish between deaths and emigrations. If the numbers of immigrations and emigrations is approximately equal, then of the 102 losses up

to 1 July, about 60 will be emigrations and 42 deaths. Losses after 1 July are almost certainly due to deaths. (See Fig.5).

TABLE 4. Total gains and losses for all ponds on different dates.

	Date						
	29/4	3-5/5	11-12/5	17-18/5	25-26/5	31/5-2/6	8-10/6
Gains	0	6	22	8	8	12	0
Losses	4	14	0	7	11	10	18

	18/6	24-27/6	1/7	8-13/7	19-20/7	28-30/7	3-5/8
Gains	0	2	2	0	0	10	14
Losses	18	12	10	12	0	2	3

If any ponds were not sampled on a given date, the totals were corrected as though all 4 ponds were sampled, for example if one pond was missed the total for the other three was multiplied by 4/3.

At Greenhole pond, since all the losses were during April and May, it is almost certain they were due to emigration by flight. Additional evidence for this comes from the individual who left Greenhole pond on 29 April and appeared in Bog End pond on 11 May. For some reason the gerrids found this pond unsuitable to stay on, and having laid some eggs migrated to other ponds. This may be because it was too small for the high initial density of gerrids (about $14/m^2$, or 1 per sq. ft.), or provided too little food, or too little vegetational cover. This is confirmed by the fact that of the 28 nymphs observed on 25 June, only one had survived to a late instar by 3 August.

FIGURE 5. Histogram showing total numbers gained and lost on successive dates for all four ponds

Key

due to immigration
due to new generation
} Total numbers gained

due to emigration deaths
due to deaths only
} Total numbers lost

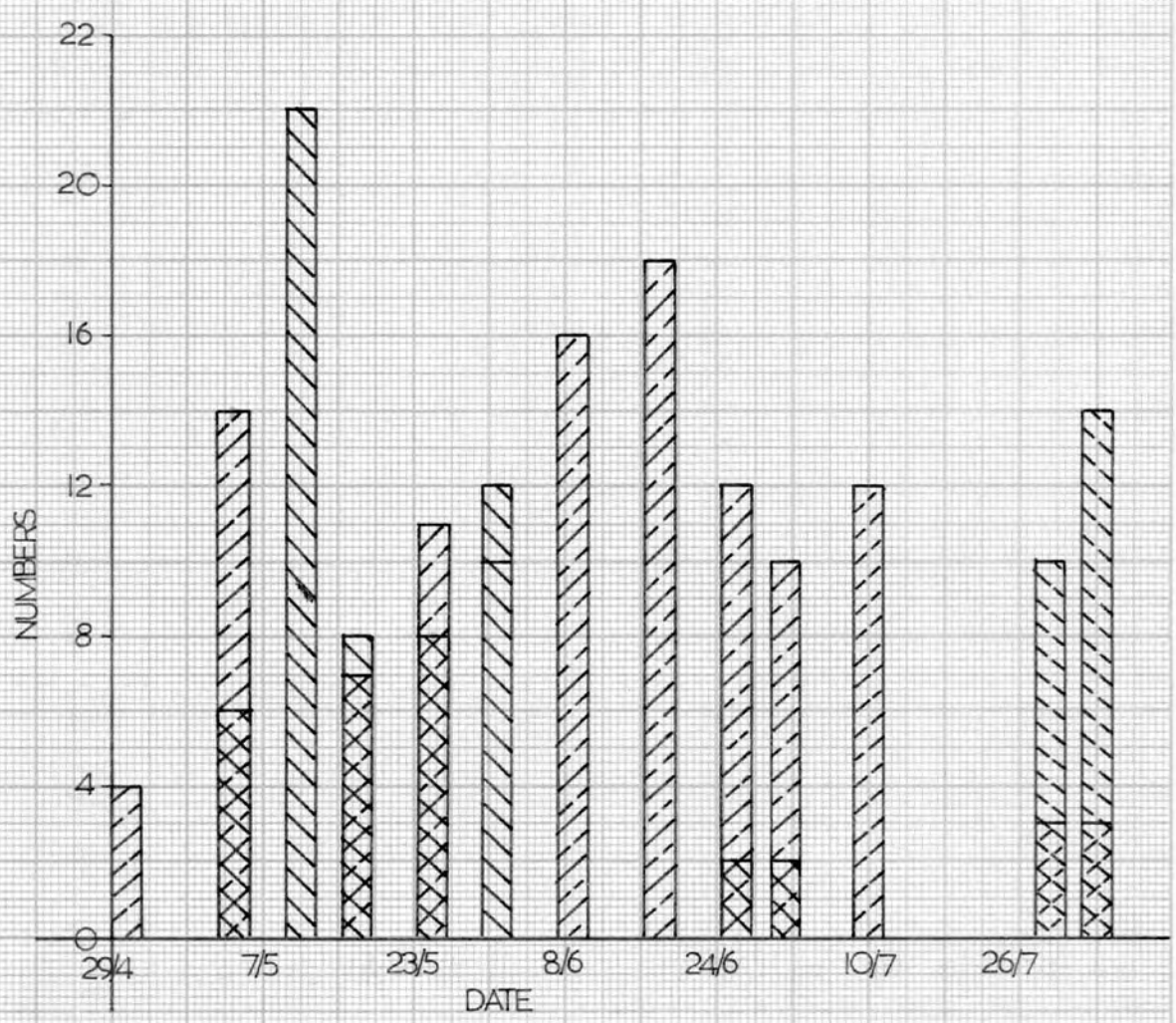

22
20
16
12
8
4
0
NUMBERS
29/4
7/5
23/5
8/6
24/6
10/7
26/7
DATE

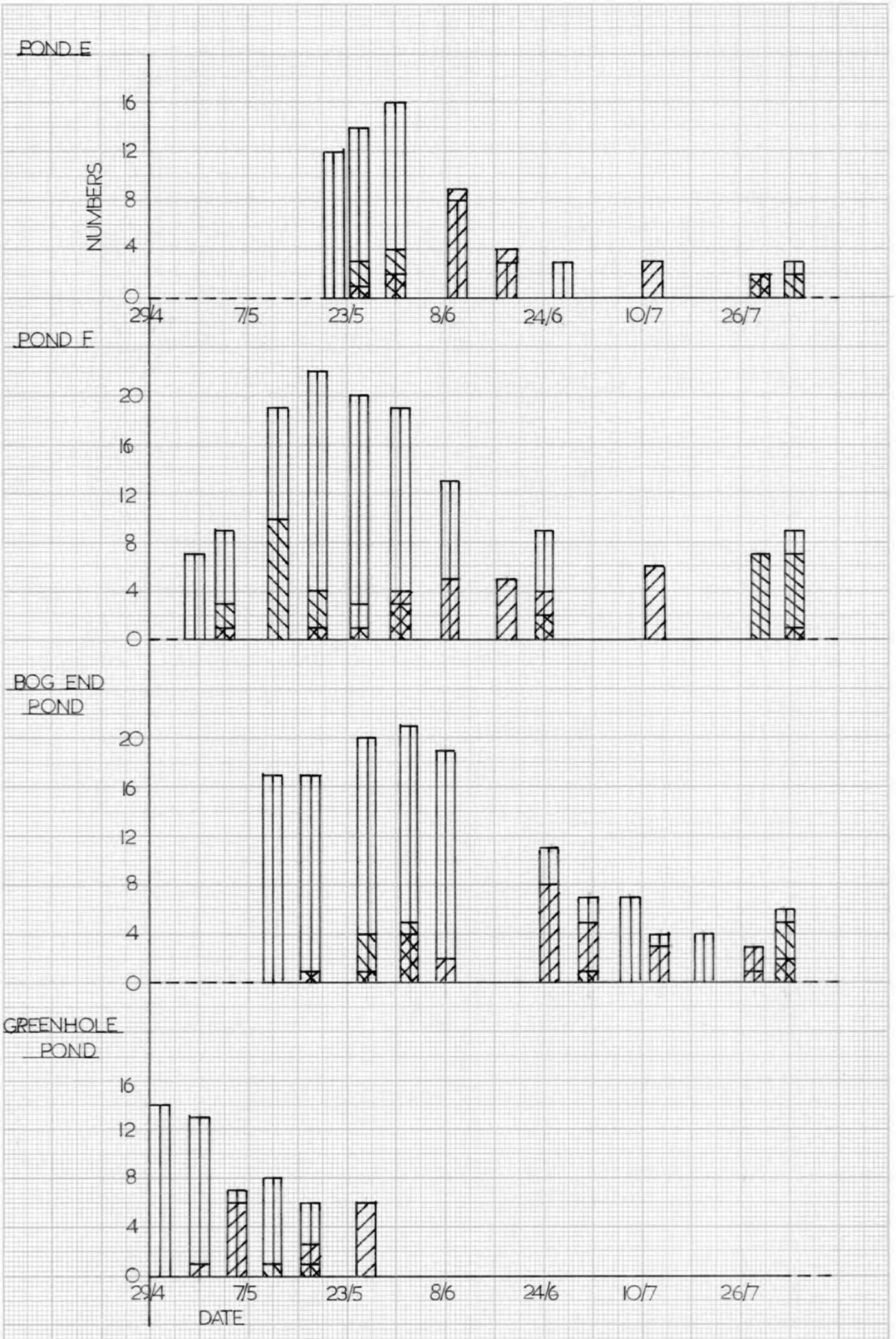
FIGURE 4. Histograms showing total numbers of gerrids present, numbers gained, and numbers lost from ponds on successive dates.

Key

Total numbers present

Total numbers gained

Total numbers lost


POND E
NUMBERS
0
4
8
12
16
29/4
7/5
23/5
8/6
24/6
10/7
26/7
POND F
0
4
8
12
16
20
BOG END POND
0
4
8
12
16
20
GREENHOLE POND
0
4
8
12
16
29/4
7/5
23/5
8/6
24/6
10/7
26/7
DATE

b) ESTIMATION OF TOTAL NUMBERS AND MOVEMENTS BETWEEN OPPOSITE SIDES OF PONDS.

Methods.

The total numbers of gerrids were estimated for ponds A, B and G. All these ponds were long and narrow (for vegetation maps see appendices 6, 7, and 12. On each sampling occasion, gerrids on the north and south sides of each pond were collected separately, and the groups given different marks. Sampling for each pond took place on three successive days. The first day the gerrids were marked and released. The second day the number of marked individuals was recorded (and also on which side they had previously been caught and marked). All those captured were given new marks. Similarly on the third day the numbers of recaptured individuals marked on each of the two previous days were recorded. On the last day, and for several days following, gerrids were collected out of ponds A and B to give an alternative value of the total numbers present.

Since individuals on opposite sides of ponds were marked differently each day, the numbers moving across each pond between sampling occasions were also estimated. The species of these individuals was recorded, though for the Lincoln index no distinction was made between species.

Results.

The numbers on each pond were estimated from the modified Lincoln index for use where the numbers of recaptures is small. Four estimates per pond were obtained from the results (which are given in Appendix 5) though P_y uses figures pooled from those used to give P_w and P_x.

$$P_w \text{ (population on day 1)} = \frac{a_1 \times (n_2 + 1)}{r_{21} + 1}$$

$$P_x \text{ (")} = \frac{a_1 \times (n_3 + 1)}{r_{31} + 1}$$

$$P_y \text{ (")} = \frac{a_1 \times (n_3 + n_2 + 1)}{r_{21} + r_{31} + 1}$$

$$P_z \text{ (" day 2)} = \frac{a_2 \times (n_3 + 1)}{r_{32} + 1}$$

where a_1 = the total number of marked animals released on the first day.

a_2 = the total number of marked animals released on the second day.

n_1 = the total number of animals captured on the first day.

n_2 = the total number of animals captured on the second day.

n_3 = the total number of animals captured on the third day.

r = recaptures, the first subscript representing the day of captures and the second the day of marking.

TABLE 5. Population estimates from Lincoln indices on ponds A, B and G on given dates.

Pond	(P_w)	Date	(P_x)	Date	P_y	Date	P_z	Date
A	55	14 June	54	14 June	55	14 June	44	15 June
B	80	14 June	111	14 June	99	14 June	94	15 June
G	30	17 June	40	17 June	31	17 June	22	18 June

TABLE 6. Total numbers collected out from ponds A and B during 16 - 24 June.

	G.odontogaster	G. lacustris	Total
Pond A	38	3	41
B	81	16	97

TABLE 7. Numbers of individuals moving between opposite sides of the ponds.

Time period:	Between days 1 and 2		Between days 2 and 3		
Species :	G. Odontogaster	G. lacustris	G. odontogaster	G. lacustris	Total No.
Pond A					
No. marked individuals moving to opposite side	4	0	6	0	10
No. marked individuals staying on same side	8	0	13	0	21
Pond B					
?	3	0	8	0	11
	6	1	13	2	22
Pond G					
?	2	0	0	0	2
	5	0	6	0	11

From this table, the proportion of marked individuals crossing the pond each day was calculated, and hence the total number of individuals crossing the pond per day was estimated (using P_Z as the total population estimate).

TABLE 8. Proportion of marked individuals and total number of individuals, crossing the pond each day; and the distances moved.

Pond	Prop. marked individuals crossing.	Total no. individuals crossing.	Distance moved
A	0.32	14	10 ft. (3m.)
B	0.33	31	14 ft. (4.2m.)
G	0.15	3	15 ft. (4.5m.)

Discussion.

The population estimates (P_y and P_z) show good correlation with the numbers obtained on collecting out ponds A and B. This correlation was better for pond B, which had a larger population of gerrids than pond A.

The results in tables 7 and 8 suggest that the opposite sides of the ponds do not support discreet populations of gerrids, but there is considerable mixing between the two sides. The extent of this mixing does not seem to be related to the distance moved in crossing over; possibly it is related to the vegetation pattern of the ponds. Ponds A and G have a high percentage cover of Potamogeton natans and both have a lower rate of crossing over than pond B, which for much of its length has stretches of clear water surface separating the two sides. This conclusion could be verified by observation from a hide over long periods.

THE DISTRIBUTION OF VELIA CAPRAI ON A SMALL STREAM.

Introduction

When Velia are present on a stream, they are not scattered evenly over the surface, but are found on slow-moving sections and near the banks. The densities of this apterous bug are controlled by the interaction of several factors, including its reactions to varying light, wind and stream speeds. Popham (1945) showed that although Velia is positively phototactic, it has great powers of adaptation to varying light conditions. His study on the effect of stream speed showed that the highest densities of Velia were present in streams with a speed of 0 to 0.3 ft (9 cm.) per sec. Densities decreased as the stream speed increased. He also showed that they have a preference for windspeeds of less than 5 m.p.h. (8 km. p.h.)

Velia tend to maintain their position in relation to a fixed point on the side of the stream, and will make frantic movements to regain their former position if displaced by the current or wind. Hence maximum numbers would be expected where there is a minimum wind and stream speed, some sunlight, and also overhanging vegetation for use as anchoring points. Popham points out that differences in rainfall alter the characteristics of a stream considerably, so no single site is always ideal for Velia. Brinkhurst (1959a) records that Velia is often found beneath tree-roots projecting into the stream. Presumably these would provide shelter from stream currents.

Roos (1957) studied the migration of stream-dwelling insects, and showed that some species move upstream prior to oviposition. This would tend to counteract the effect

of eggs and larvae being carried downstream by the current.

The purposes of this experiment were to determine the numbers of Velia at different points on a stream and estimate migration up and downstream.

Methods.

The stream used for this study was at the University Field Station, Durham. Five sites were chosen along the length of the stream, each having a reasonable population of Velia concentrated in a small area. (See Fig.3). At weekly intervals, all the visible adult Velia at each site were captured, the number of marked ones recorded, and unmarked ones given marks. The marks applied at each site were the same every week, since Velia does not lend itself to being marked more than five times. In practice the recaptures were considerably fewer than anticipated from general observation, so none would have needed to be marked this many times. After marking, the bugs were released at the same sites. No nymphs later than the third instar were observed during this experiment, so there was no immigration due to 'births'.

Results (See Appendix 6). For distances between sites, see Fig.3.

Site (1) covered an area of 20 sq.ft. (1.8 m^2), was sheltered by steep banks and received patches of sunlight. The overhanging vegetation was Dactylis glomerata, Juncus effusus, and Urtica.

Site (2) covered about 10 sq.ft. (0.9 m^2) was a little less sheltered than site (1), and received direct sunlight all over its area. The overhanging vegetation was Juncus effusus, and Dactylis glomerata, and Nasturtium officinale

grew in the water.

Site (3) was about as sheltered as site (2), and covered 10 sq.ft. (0.9 m^2). It received patchy sunlight and had a small amount of overhanging vegetation, chiefly Juncus effusus. On 19 and 27 May the water level was well below that of the overhanging vegetation.

Site (4) consisted of an area of clear water in the pond, covering 30 sq.ft. (2.7 m^2). Most of the area received direct sunlight and the surrounding vegetation was Dactylis glomerata, Nasturtium officinale and Ranunculus. There was also a population of Gerris lacustris and a few G. lateralis on the pond.

Site (5) covered 20 sq.ft. (1.8 m^2), and was situated just above the lower dam. It received no direct sunlight and had no overhanging vegetation; there were steep banks of earth on each side.

Out of 508 individuals marked altogether, only four movements between sites were recorded. These were all from site (2) to site (3), a distance downstream of about 82 ft. (25 m). They were recorded on 16 April (one individual), 22 April (one individual) and 4 May (2 individuals). There were no recorded movements upstream. It can be concluded that in this situation movement both up and downstream was negligible.

Population estimates were made for each site on successive weeks using a Lincoln index, incorporating the correction factor for use where the number of recaptures is small:

$$P = \frac{a\,(n + 1)}{r + 1}$$

where a is the accumulated total number of animals marked at the site up until the previous week, n is the total number of animals captured at the site on the present date, and r is

the number of those captured which were already marked. For values of a, r and n see Appendix 7.

TABLE 9. Weekly estimates of P at different sites on the stream.

	(1)	(2)	(3)	(4)	(5)
16 April	240	90	84	(84)	
22 April	600	410	155	(209)	(161)
4 May	724	221	143		(232)
12 May	397	327	131		276
19 May	388	231	256	160	(1512)
27 May	488	490	(67)	209	(656)
Mean values:	473	298	154	185	276
Density (no. per sq.ft.)	24	30	15	6	-
(no. per sq. m.)	262	331	172	69	153

The estimates in brackets are those for which the number of recaptures was zero, and hence the figures are unreliable. These are not included in the mean values. There were only two recaptures altogether from site (5), both on 12 May. It is likely that this population was part of a much larger one in the area by the dam, which could not be reached for sampling.

There is a general pattern at all sites of low initial numbers on 16 April rising to a fairly steady level as Velia come out of hibernation.

Discussion of densities at different sites.

The conclusions of Brown about the effects of light, wind and water speeds on Velia density are borne out well by these results. At all sites the water speed was normally

within the range 0 to 0.3 ft. (9 cm.) per sec., and so water speed was not a limiting factor in this situation. The pond, (site (4)) was the most exposed to wind, and also had the lowest densities of Velia. However, inter-specific competition with Gerris might also be producing these low densities. The pond received plenty of sunlight, but it seems that where the other factors are unfavourable sunlight does not result in high densities. At site (2) however, plenty of sunlight, combined with shelter from wind gave rise to the highest densities of Velia.

2) ESTIMATION OF POTENTIAL FOOD

Review of literature.

Gerrids are known to feed chiefly on terrestrial insects which fall onto the water and float on its surface. (Curtis Riley 1918). Lumsden (1949) recorded the prey species of *Gerris najas* in boathouses on the shores of Lake Windermere. He captured 32 specimens belonging to the following taxonomic groups: Chilopoda, Hemiptera, Neuroptera, Coleoptera, Hymenoptera and Diptera. All the specimens were fairly soft-bodies and "small or very small." 23 out of the 32 were decayed, indicating that gerrids have a preference for food which is already dead. The gerrids most active feeding period coincided with an offshore wind, which in the tree-fringed locality being studied by Lumsden, allowed the settling of wind-carried objects. The gerrids orientated to face upwind.

The literature contains very little reference to the diurnal activities of gerrids. Flight has been observed on moonlit nights (Curtis Riley 1921) as well as during the day, but since sight plays an important part in hunting when the gerrid is within 20 cm. of its prey (Southwood and Leston 1959), it seems likely that most feeding is done during daylight hours.

Aims and Methods.

It seemed likely that the amount and composition of potential food falling onto a pond might be an important factor governing the numbers of the different species of *Gerris* on the pond. To examine this relationship, the potential food falling onto each of a series of ponds was estimated, and this information

coordinated with other experiments on estimated numbers of Gerris present on the ponds. It was thought that overhanging vegetation might be an influence on potential food, so the traps used were designed to collect animals reaching the water surface via the vegetation, and also those landing directly on the water surface, in separate compartments.

The traps consisted of plastic boxes, 11" long x 7" wide x 5" deep (28 x 18 x 13 cm.) with a perspex partition down the centre; weak detergent solution was put in both compartments. When in position, the trap had vegetation draped over one side of the box and not the other.

Six ponds at Brasside and one at Moorhouse were chosen for their varying size, vegetation pattern, and degree of exposure to wind. One trap was placed in each pond. At each collection the contents of the two compartments were emptied separately, (by siphoning with a polythene tube) filtered, and preserved in alcohol, and the numbers of specimens in different orders counted. Two schemes of collections were followed:-

1) The traps were emptied at 8-hourly intervals (8.00, 16.00 and 24.00 hours) for two consecutive days.

2) The traps were emptied after one week for four one-week periods, though these were not continuous, as the traps were used for scheme 1, which was fitted in between the first and second of the weekly periods. The dates of the weekly collections were 28 June, 12, 19 and 25 July. Only one weekly collection was made at the Moorhouse pond (25/7), and the effect of over-hanging vegetation was not estimated in this trap.

Results.

These are given in appendices 7 and 8.

Calculations.

The results for the weekly collections contained four variables: ponds (A-F), dates (see above), orders of animals present, and lastly whether the collection was from the vegetation side of the trap or the other side (here referred to as veg./non-veg.) For the 8-hourly collections there were three variables: time (8.00, 16.00, 24.00 hours), ponds (A-F) and lastly orders of animals present. For each experiment the data were pooled so that the factors could be examined two at a time, giving the tables shown in appendices 9-15. Where appropriate, values of χ^2 were calculated on the various totals, and also percentages, where these clarified the situation. The veg./non-veg. factor was obviously operating in a different manner on each pond, and among the orders of animals, so χ^2 values were calculated for the totals from individual ponds and orders. The results for the Moorhouse pond were not included in these calculations, but merely included here for comparison.

The areas of ponds were estimated by drawing maps to scale on graph paper, and counting the squares. From the mean totals per week on each pond, and the area of the trap (0.516 sq.ft. or 0.45 m) the total potential food entering each pond per week was estimated. (See Table 10). Correlation coefficients were calculated for the relation between (1) the area of each pond and the mean numbers of food per week in the trap; and (2) the circumference of the pond and the mean numbers

of food per week in the trap. Although neither value of r is significant, there is a slight indication that had more data been available the mean numbers of food per week might have been inversely proportional to the circumference and area of the pond. (See Figs 15 and 16).

TABLE 10. Numbers of food in relation to area and cirumference of the ponds.

Pond	Circumference (m)	Area (m^2)	Circumference/ area	Mean nos. food per week in trap.	Mean nos. food per week for whole pond.
A	38	42.1	0.90	156	14,140
B	85	108.5	0.79	135	31,570
C	23	24.3	0.95	171	8,940
D	12	4.1	2.93	160	1,396
E	13	6.9	1.88	196	2,924
F	14	11.0	1.27	230	5,440
Moor-House pond	8	4.5	1.78	62	601

Discussion.

1) 8-hourly collections.

The total food coming in reaches a peak between 8.00 and 16.00 hours and a minimum between 16.00 and 24.00 hours. This pattern also occurs in the order Diptera which make up a major part of every sample. For three of the ponds the differences between totals at different times were not statistically significant; these ponds had the lowest totals, and larger samples would almost certainly have shown a significant difference. Of the ponds with a significant difference between totals at

different times, two showed a peak between 8.00 and 16.00 hours and one between 24.00 and 8.00 hours. This could be due to local differences in any of several factors, and conclusions cannot be drawn from the comparison of only three ponds.

If Gerris do most or all of their hunting by day, they are clearly well adapted to make maximum use of this peak in potential food during daylight hours. It would be difficult to study their hunting activities at night, since they are positively phototactic. (Curtis Riley 1921).

2) Weekly collections.

The totals from all ponds for different weeks are clearly different, but show no definite trend. The totals in different ponds are also obviously different, but are related in roughly the same proportions to each other in different weeks. The different ponds received food of roughly similar composition with regard to orders, and there was little difference in the composition of food in different weeks.

Hence, of the various factors examined, that of veg./non-veg. seems to contribute most to the differences on each pond. There was no clear-cut indication that overhanging vegetation generally increased or decreased the amount of food; on two ponds it increased the amount of food, on two ponds it decreased it, while on a further two it made very little difference. This was possibly because of the differences in vegetation used for the overhanging, and also possibly because of other factors not directly examined, such as exposure to wind, direction of wind, together with amount of vegetation

in the surrounding area of a sufficient height to harbour large numbers of insects and other potential food.

On pond A, the 'overhanging' vegetation was Potamogeton natans. The increase in food on the veg. side of the trap indicates that live animals used the Potamogeton as a ladder into the trap. This has important implications about the availability of such live food to Gerris. It is likely that prey can escape more easily on a surface largely covered by Potamogeton than on a clear water surface, on which they more easily become trapped. Gerris are more agile on a clear water surface than on a surface covered by Potamogeton. Pond A was the second to largest pond, and although in a very exposed position is surrounded mostly by vegetation no more than 3" (8 cm.) high. This would account for the comparatively low numbers of potential food. On pond B, the largest pond, the overhanging vegetation was Juncus effusus. Although the pond itself had a fringe of Juncus all round its perimeter, it was in a very sheltered position, with steep banks about 8 ft. (2.4 m) high. At the top of the bank at the end where the trap was positioned there were some hawthorn trees. It seems that more food came into the non-veg. side of the trap because the other side was effectively shielded from food coming in from the trees by the Juncus. The sheltered position of this pond might account for the low numbers of potential food.

Pond C was in a very exposed position, surrounded by a lot of vegetation up to 2 ft. (60 cm.) in height, and so this could explain the fairly high numbers of food. Again, the overhanging vegetation was Juncus effusus, which had a shielding effect on this side of the trap.

Pond D was in a sheltered position under a hawthorn tree. A large proportion of the pond area was covered by Juncus effusus, which was used as the overhanging vegetation. The non-veg. side was unavoidably shielded to some extent by the Juncus. It seems likely that potential food fell from the tree into the Juncus. From here some of it moved via the overhanging Juncus into the trap.

Pond E was a small, long and narrow pond, so that all the surface was fairly near the surrounding vegetation. So whatever the wind direction, potential food is brought into the pond. It is surrounded by vegetation up to 3 ft. (90 cm.) high. Under these conditions the fact that one side of the trap had Juncus hanging into it made little difference to the amounts in each side of the trap.

Pond F was in a very exposed position surrounded on three sides by vegetation about 18" (45 cm.), and so received the highest numbers of food. The 'overhanging' vegetation was Equisetum sp., bent into the trap. This grew very sparsely all over the pond, and probably had the effect of causing wind carried objects to settle on the pond. There was very little floating vegetation, so live food was probably trapped on the water surface.

These observations suggest three things:-

1) The presence of Potamogeton natans provides a sancuary for live potential prey to stay alive without becoming trapped on the water surface.

2) Small ponds, with a larger perimeter/surface area probably receive more food per area than do large ponds, all other factors being equal.

3) The amount of potential food is probably influenced by factors other than those directly studied here, such as exposure to wind, and amount of vegetation in the area which could as a reservoir for potential food.

3) THE NUMBERS OF GERRIDS ON DIFFERENT PONDS IN RELATION TO POTENTIAL FOOD AND VEGETATION PATTERN.

Methods.

Seven ponds at Brasside were chosen for this study. For six of these, ponds A - F, estimations of the potential food available for gerrids had been obtained (see section III,2), and the seventh, pond G, had a vegetation pattern slightly different from the other six.

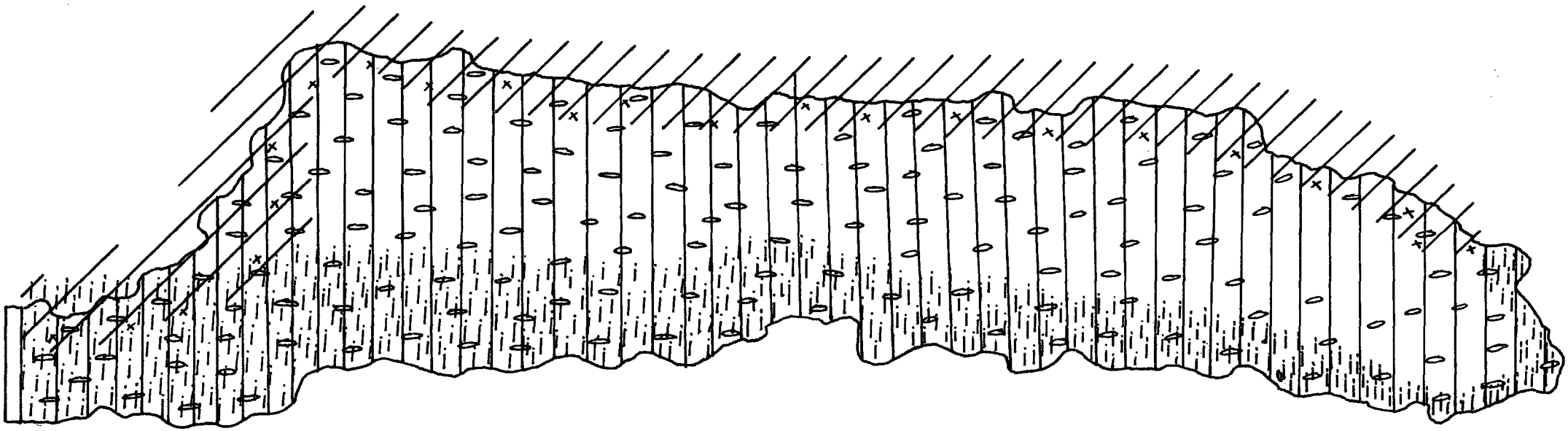
The numbers of each species of gerrid on the ponds were counted by eye, on a fine day (26 August). This method was considered the most satisfactory in the time available, since when gerrids are captured with a pondnet, the rest of those present on the pond become more active and difficult to catch. For each pond sketch maps were drawn showing the various plant species present, and their distribution; the percentage cover of each species of floating vegetation, and the distance into water of the standing vegetation. (See Figs. 6-12).

Results.

These are given in Table 11. Correlation coefficients were calculated for the density of gerrids versus each of the various factors, and also the ratio between numbers of *G. lacustris* and *G. odontogaster* versus each factor. The only correlation with a significant value was that between the density of gerrids and the distance into water of standing vegetation, significant at the 2% level of probability. (See Fig. 17). However, some other conclusions may tentatively be drawn from the results.

TABLE 11. Numbers of gerrids on various ponds in relation to pond size, vegetation pattern, and potential food.

Pond	A	B	C	D	E	F	G
Area (m^2)	42.1	108.5	24.3	4.1	6.9	11.0	65.0
Circumference (m)	38	85	23	12	13	14	50
Nos. gerrids (*G.odontogaster*	35	144	20	0	1	20	30
Nos. gerrids (*G.lacustris*	1	16	2	0	4	7	10
No. *G.lacustris*/No. *G.odontogaster*.	0.03	0.11	0.10	-	4.00	0.35	0.33
Density of gerrids (per m^2)	0.86	1.48	0.91	0.00	0.72	2.46	0.62
Food nos. per trap	156	135	171	160	196	230	-
%age cover *Potamogeton natans*	70	50	5	0	0	5	30
%age cover *Ricciocarpus natans*	80	90	0	0	0	0	0
%age cover *Lemna minor*	1	0	0	100	0	0	0
%age cover *Lemna trisulca*	0	0	2	0	0	5	0
Distance into water of standing vegetation (m.)	1.0	1.0	1.3	0.6	0.6	2.0	0.6



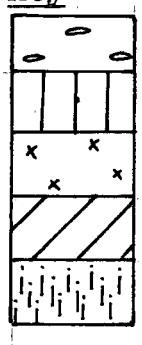
Scale:

0 1·2

metres

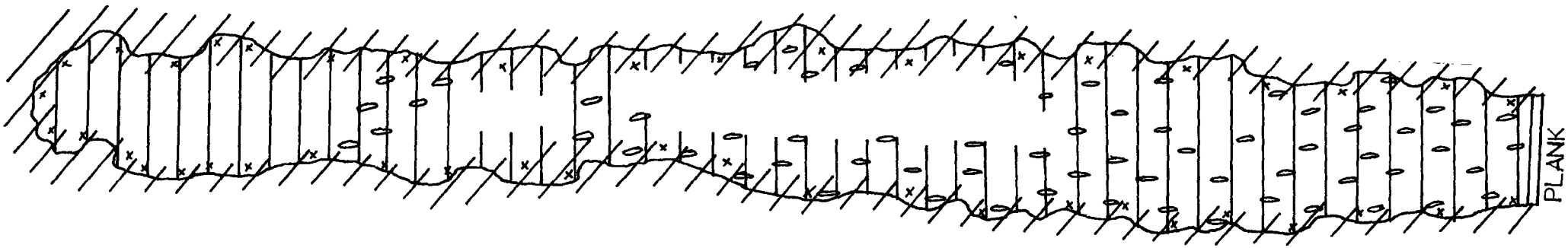
FIGURE 6. Sketch-map of pond A

Key



Species	%age cover
Potamogeton natans	70
Ricciocarpus natans	80
Lemna minor	1
Juncus effusus	
Eleocharis palustris	

Distance into water of standing vegetation: 1.0m

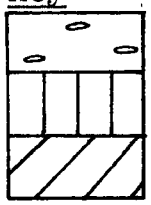


Scale:

0 3

metres

FIGURE 7. Sketch-map of pond B.

Key	Species	%age cover
	Potamogeton natans	50
	Ricciocarpus natans	90
	Juncus effusus	

Distance into water of standing vegetation: 1.0m

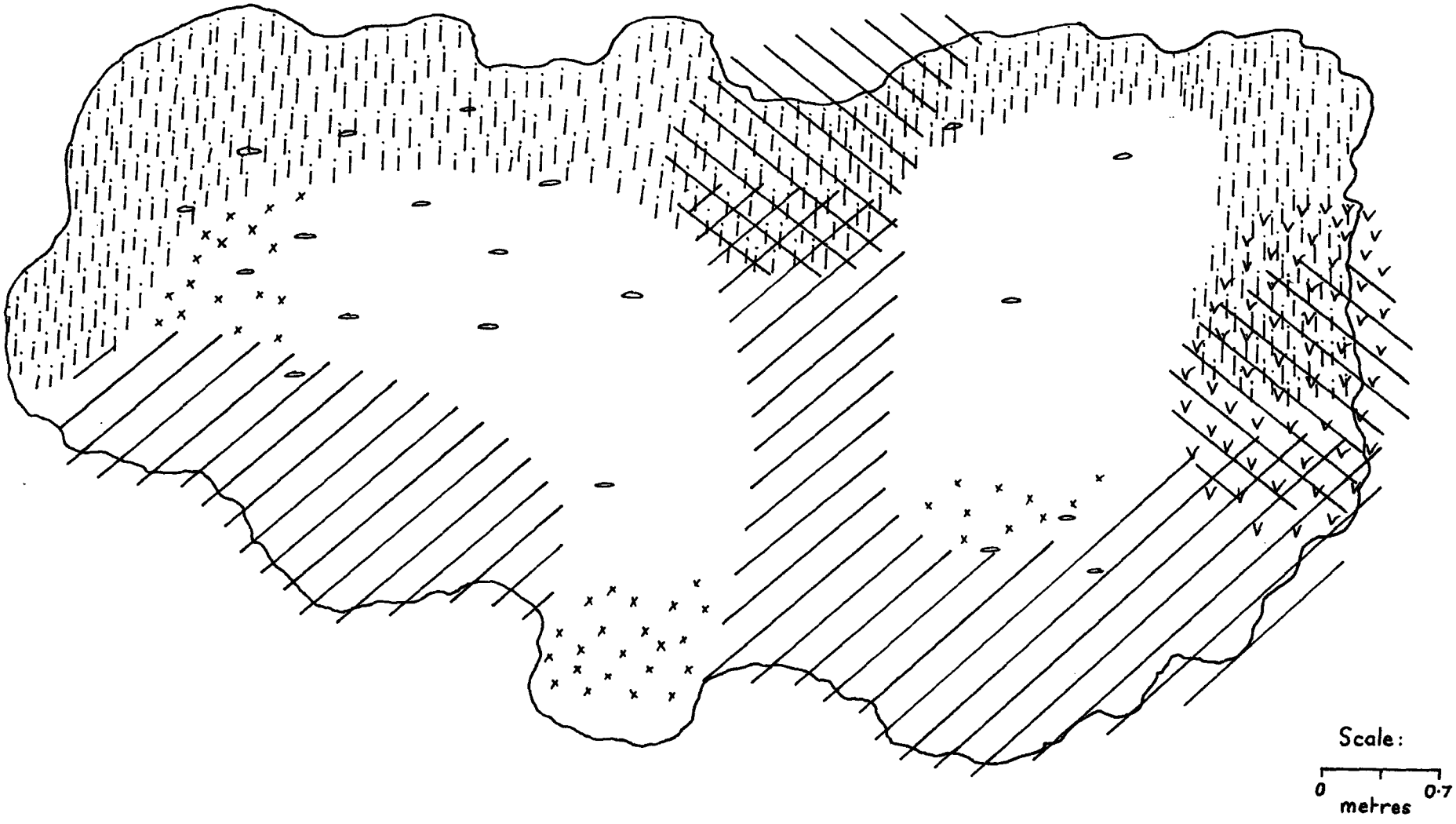
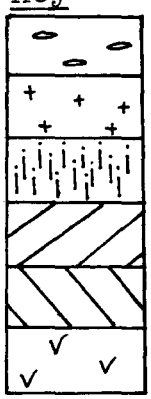

Scale:
0
0·7
metres

FIGURE 8. Sketch-map of pond C.



Key	Species	% age cover
	Potamogeton natans	5
	Lemna trisulca	2
	Eleocharis palustris	
	Juncus effusus	
	Juncus squarrosus	
	Equisetum sp.	

Distance into water of standing vegetation: 1.3m

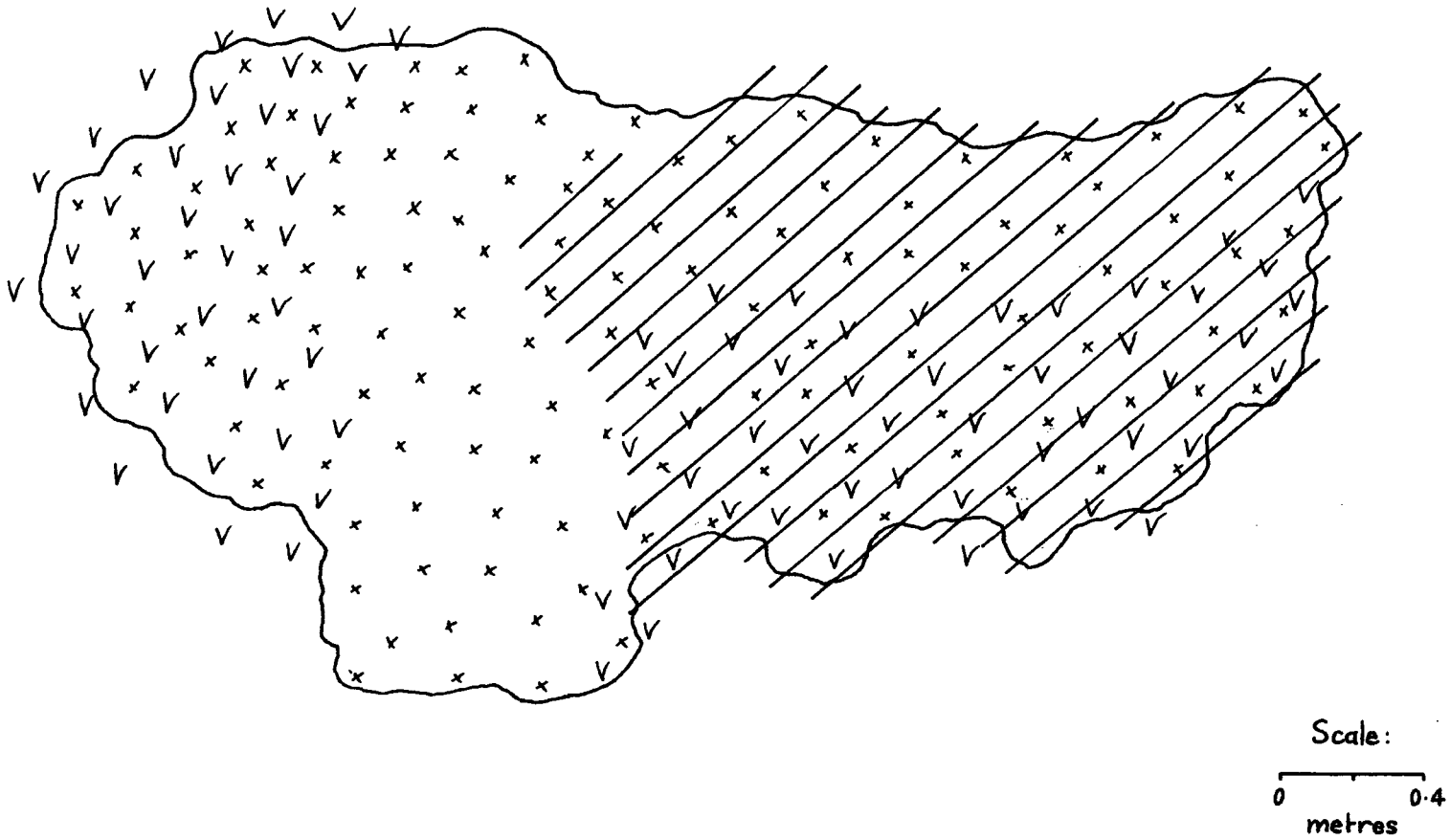
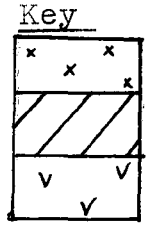

Scale:
0
0·4
metres

FIGURE 9. Sketch-map of pond D

Key	Species	%age cover
	Lemna minor	100
	Juncus effusus	
	Equisetum sp.	

Distance into water of standing vegetation: 0.6m

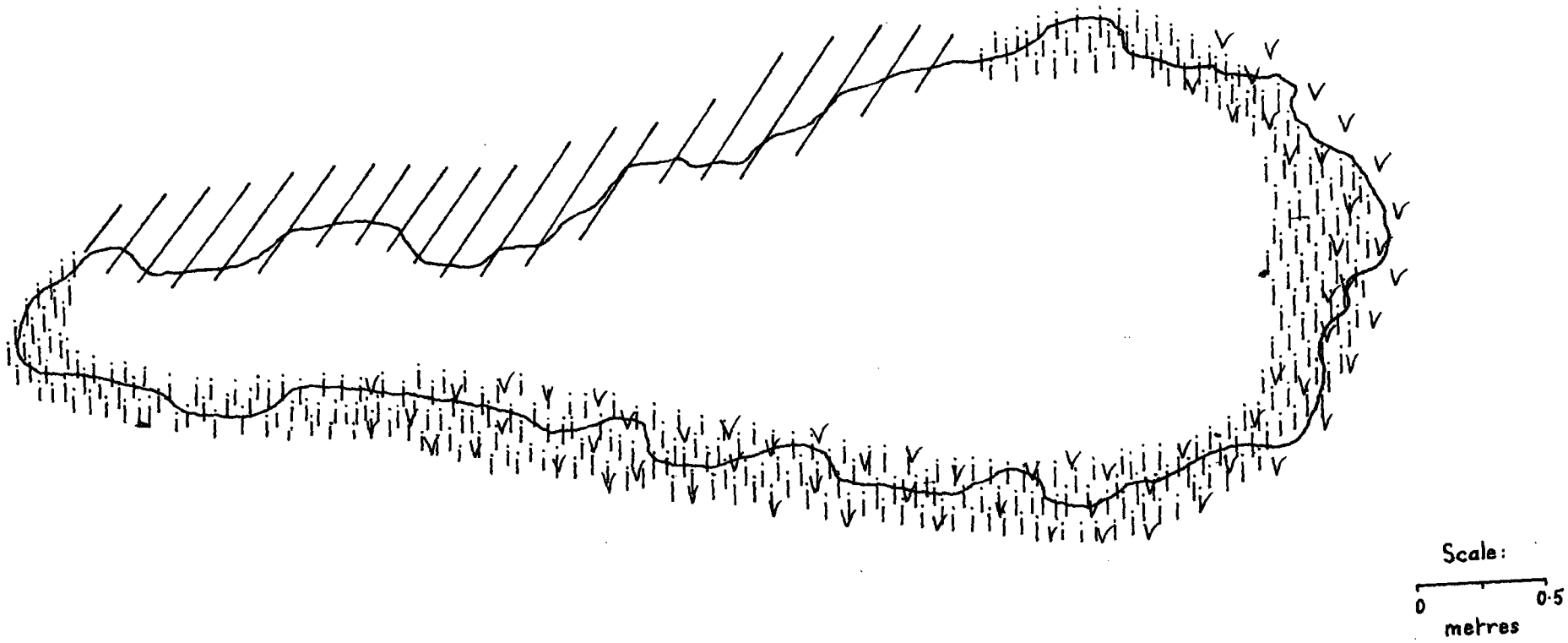
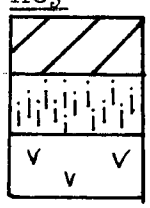

Scale:
0
0·5
metres

FIGURE 10. Sketch-map of pond E.

Key



Species

Juncus effusus

Eleocharis palustris

Equisetum sp.

Distance into water of standing vegetation: 0.6m

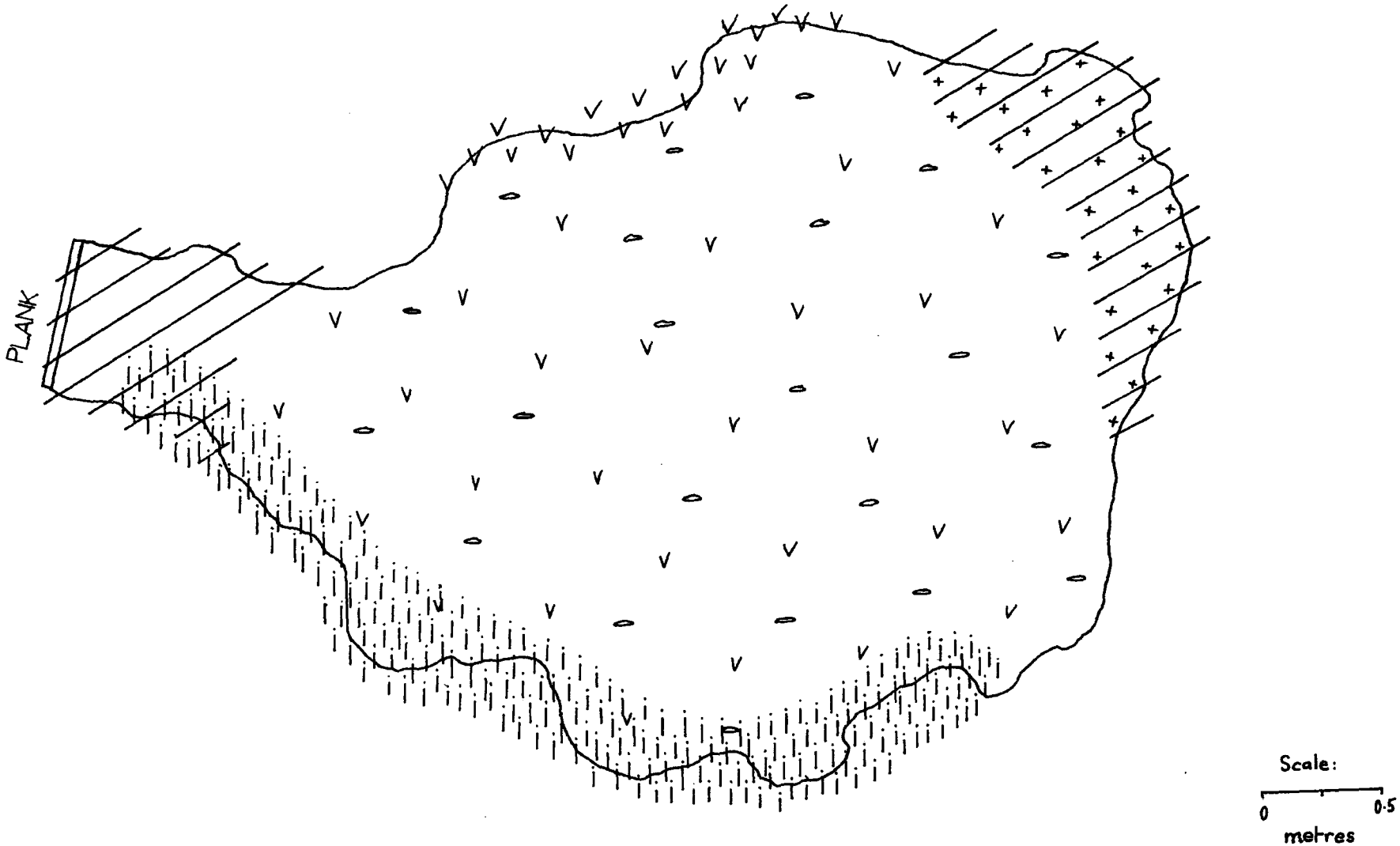
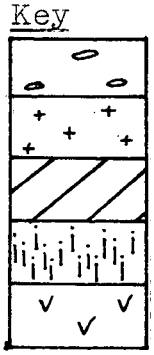

PLANK
Scale:
0
0·5
metres

FIGURE 11. Sketch-map of pond F.

Key



Species	%age cover
Potamogeton natans	5
Lemna trisulca	5
Juncus effusus	
Eleocharis palustris	
Equisetum sp.	

Distance into water of standing vegetation: 2m

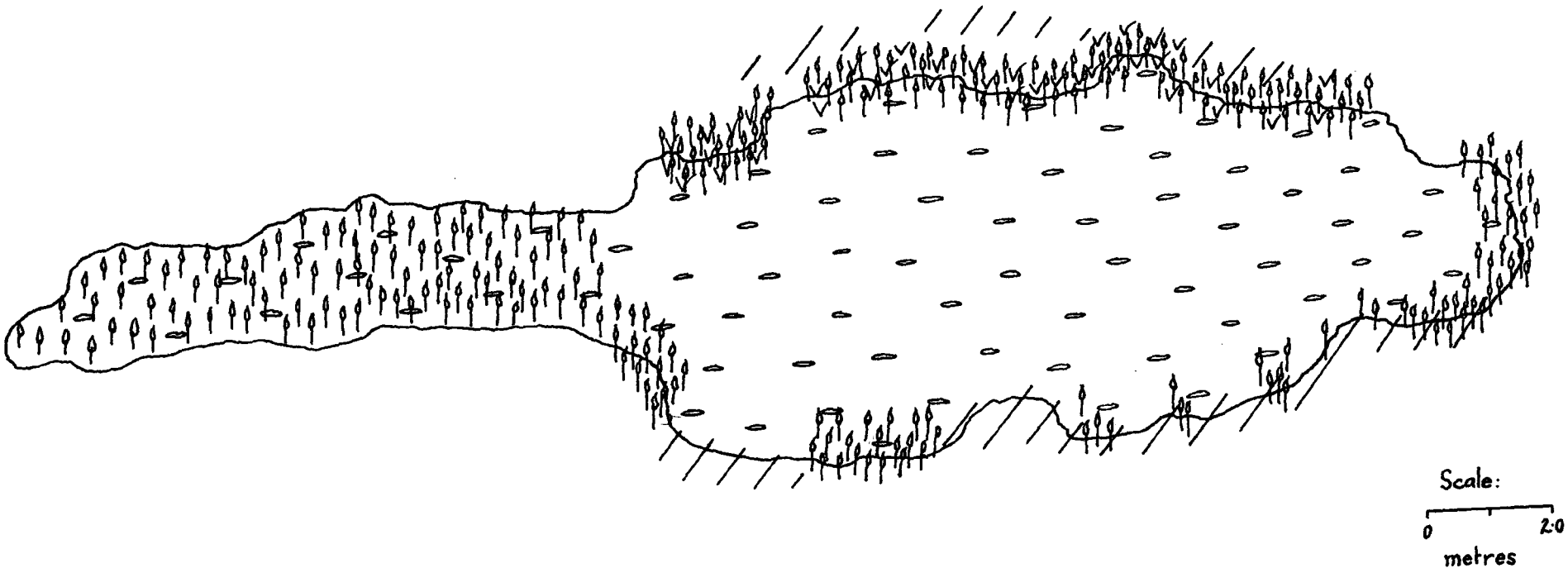
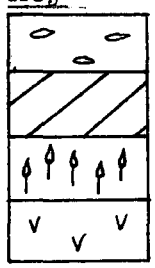

Scale:
0
2·0
metres

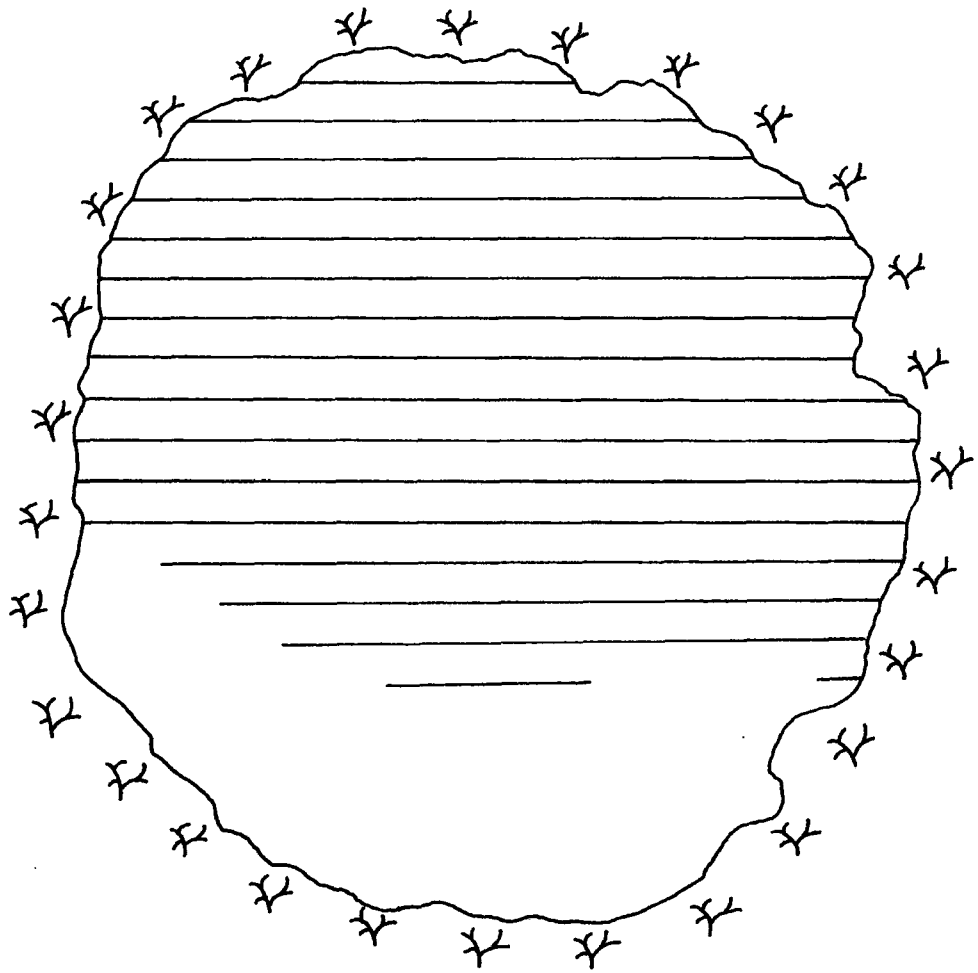
FIGURE 12. Sketch-map of pond G.

Key



Species	%age cover
Potamogeton natans	30
Juncus effusus	
Alisma plantago-aquatica	
Equisetum sp.	

Distance into water of standing vegetation: 0.6m

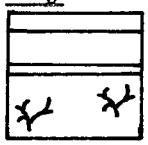


Scale:

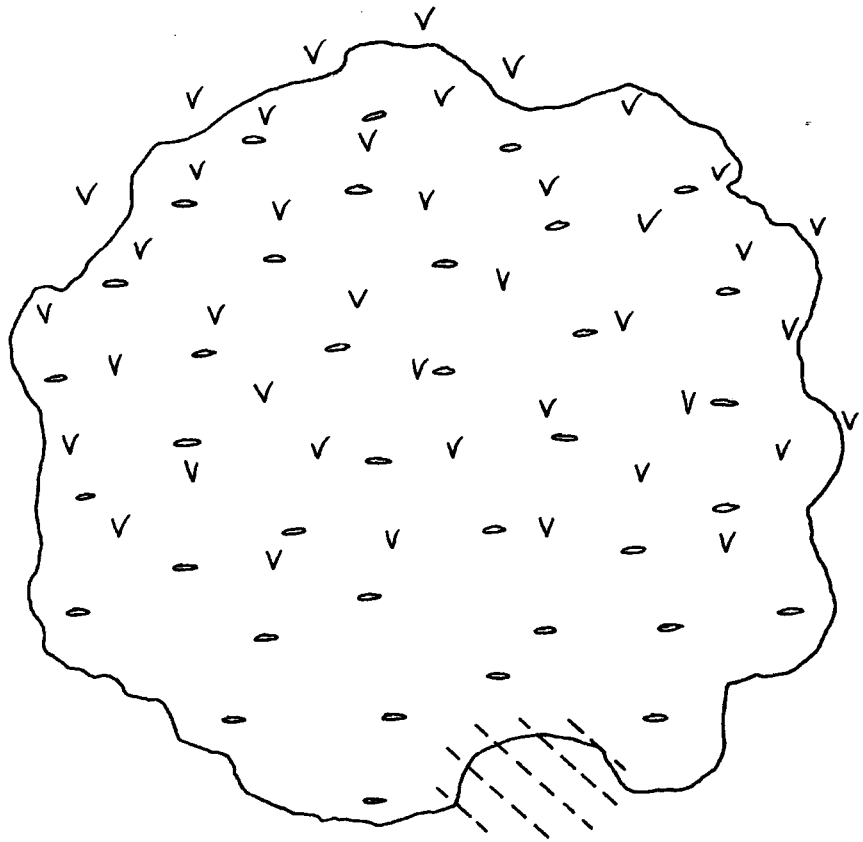
0 0·5

metres

FIGURE 13. Sketch-map of Greenhole pond.

Key	Species	%age cover
	Sphagnum sp.	80
	Calluna vulgaris	

There was no standing vegetation in this pond.



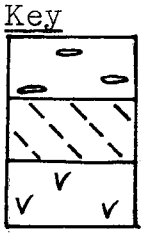
Scale:

0 0·4

metres

FIGURE 14. Sketch-map of Bog End pond.

Key



Species	%age cover
Potamogeton natans	30
Juncus conglomeratus	
Equisetum sp.	

Distance into water of standing vegetation: 1.6m

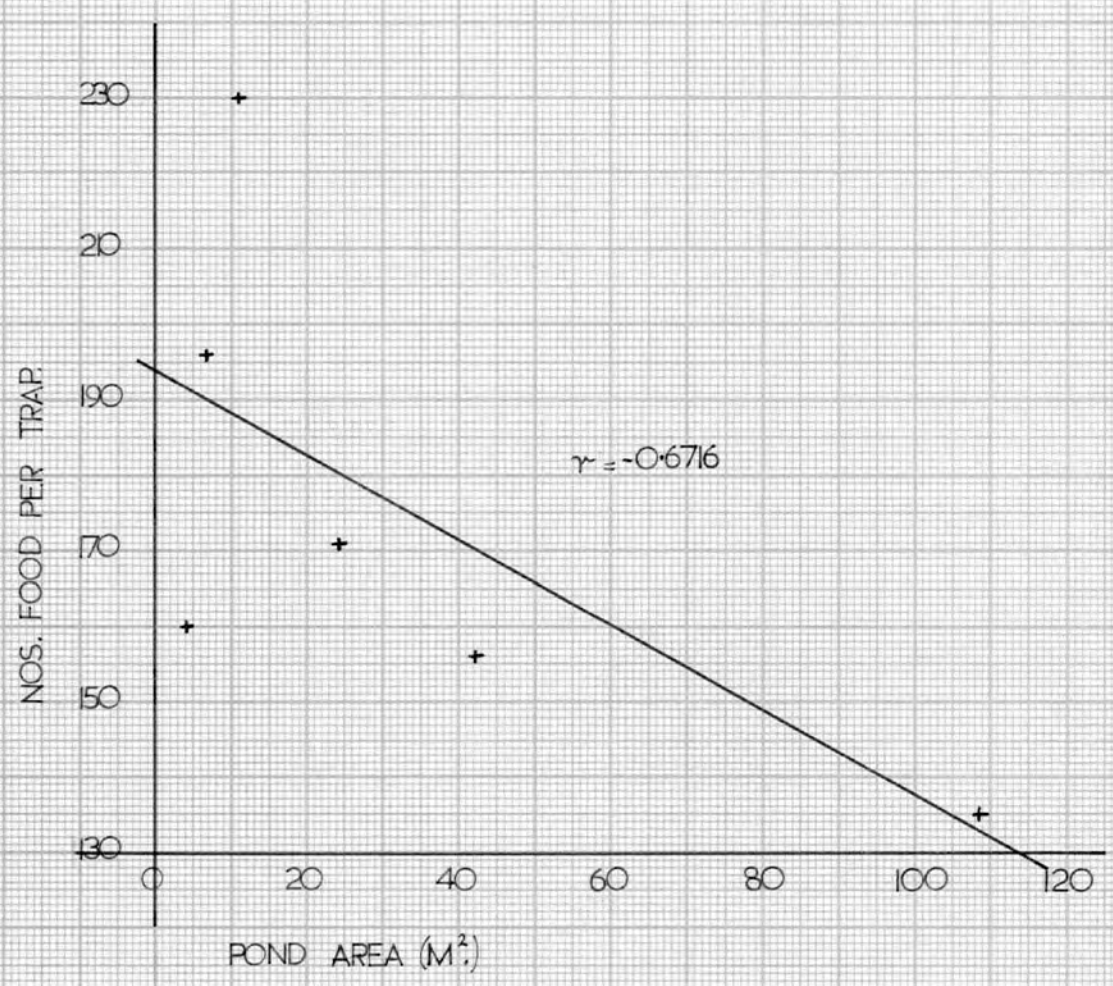

230
210
190
170
150
130
NOS. FOOD PER TRAP
r = -0·6716
0
20
40
60
80
100
120
POND AREA (M²)

FIGURE 15 Graph showing correlation coefficient for: Area of pond versus numbers of food in trap.

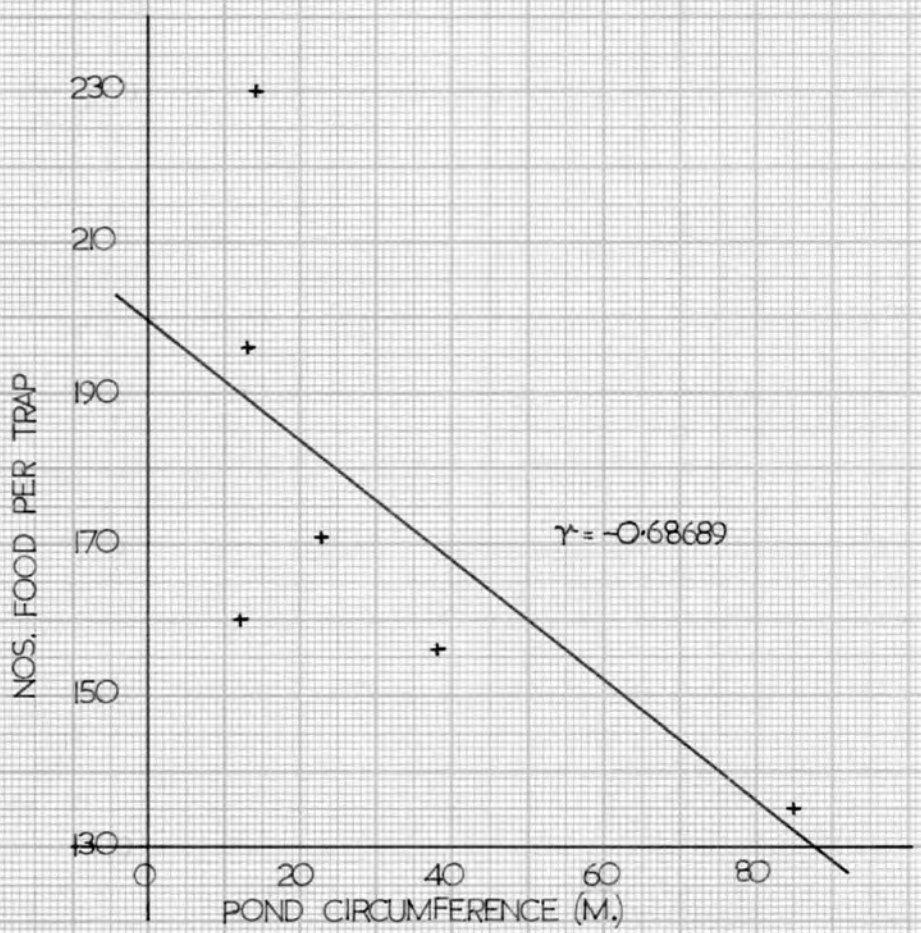

230
210
190
170
150
130
NOS. FOOD PER TRAP
r = -0·68689
0
20
40
60
80
POND CIRCUMFERENCE (M.)

FIGURE 16. Graph showing correlation coefficient for: Circumference of pond versus numbers of food in trap.

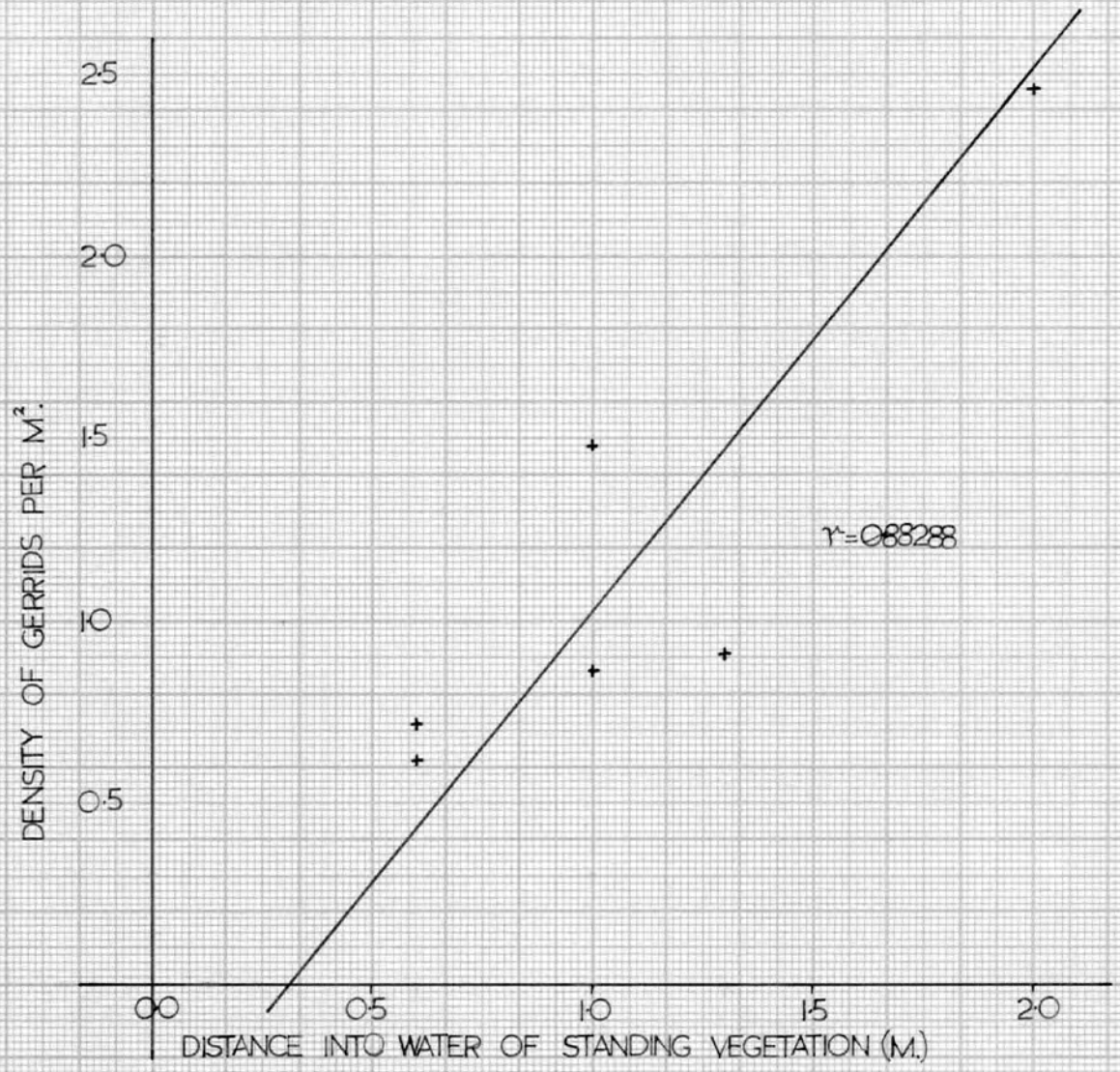

2·5
2·0
1·5
1·0
0·5
0·0
0·5
1·0
1·5
2·0
DENSITY OF GERRIDS PER M².
DISTANCE INTO WATER OF STANDING VEGETATION (M.)
r=0·88288

FIGURE 17. Graph showing correlation coefficient for: Density of gerrids on pond versus distance into water of standing vegetation.

Factors affecting density of gerrids.

There is no clear correlation between the amount of food available and the density of gerrids, hence the amount of food is not a limiting factor for these ponds. The presence of Lemna minor on a pond causes gerrids to avoid it. However Lemna trisulca is tolerated by gerrids, possibly because it is mostly submerged just below the water surface, whereas L. minor floats on the surface. The floating moss Ricciocarpus natans is tolerated even when it covered 90% of the pond (B). Potamogeton natans is tolerated up to about 50% cover. The major vegetational factor affecting the density of gerrids is the distance into water of the standing vegetation.

The ratio between numbers of G. lacustris and G. odontogaster.

The ponds fall into two groups with regard to this ratio; ponds A, B and C have a low ratio and ponds E, F and G a high ratio of G. lacustris to G. odontogaster. This division is related to the distance into water of standing vegetation, the first group having wide fringes of standing vegetation, and the second group narrow fringes. For pond F, although the distance into water of standing vegetation was 2m, most of this was very sparsely distributed stems of Equisetum sp., the fringes of Juncus effusus being not more than 0.6m.wide. This indicates that G. lacustris has a preference for ponds without a wide fringe of vegetation with closely-parted stems such as Juncus effusus and Eleocharis palustris. G. odontogaster seems to have a preference for ponds with a wide fringe of any type of standing vegetation. Pond F meets the requirements of both these species, and hence it has the highest densities of both species.

4) EGG-LAYING OF INDIVIDUAL FEMALES.

Introduction

Southwood and Leston (1959) give a summary of work on the life cycles of Gerris and Velia. Table 12 summarises this information (and gives the appropriate authors) with regard to the species studied in this experiment:-

TABLE 12. The life cycles of species of Gerris and Velia studied in this experiment.

Species	No. generations / year	Time of egg-laying	Period of development of eggs	No. eggs laid.
Velia caprai	1 or occasionally 2. (Brown 1948; Walton 1943; Wesenberg-Lund, 1943)	Late May and early June. (Brown 1948; Wesenberg-Lund 1943)		
Gerris lateralis	1 (Southwood and Leston 1959)			At least 100. (Southwood and Leston (1959)
Gerris costai	1 (Poisson 1924)	Early or mid-summer (Poisson 1924)	12-14 days at 12°-14° C. (Poisson 1924)	
Gerris odontogaster	2 (possibly 1 in the north) (Jordan 1943)	April-May and July-August (Jordan 1943)		

Southwood (1968) describes how for insects which lay their eggs in large batches, the weight of the individual female falls sharply after each oviposition, and slowly rises again until the next group is deposited. There was no indication in the literature as to whether Gerris lay their eggs in large batches or gradually over a period of time. Brinkhurst (1958) found the rearing of nymphs in the laboratory very difficult since cannibalism is common among them.

An experiment was set up to determine:-

1) over what period of time the individuals of the various species lay their eggs, and whether or not this has any relation to loss or gain in weight;

2) the number of batches laid by the different species.

Methods.

A number of individuals of each of the species present at Brasside, Moorhouse and Durham Field Station were brought back live from the field. Cultures were set up in 5" diameter glass jars, with only about 5 ccs. of water in the bottom, and a few blades of grass. A male and female of the same species was placed in each jar. The jars were kept out of doors at South End House, Durham, under cover, each with the lid of the jar placed loosely on top of the jar to prevent escapes and keep dust out. The gerrids were fed on wingless Drosophila (a mutant strain). Although constant numbers were given to each individual the Drosophila varied in size, hence the amount of food given was not exactly constant. Also since the male and female were fed together, it was not possible to ensure that the food was shared equally. Initially the jars were examined every 2 days, though later in the experiment the interval was longer.

Each time, the female was removed from the jar, dried gently on tissue and weighed to the nearest milligram. The whole jar and also the blades of grass were inspected and the number of eggs counted; the female was then returned to the jar together with the ration of food. Dead gerrids were removed. Once the eggs had begun to hatch the adults were removed to another jar, in the hope that the nymphs would develop. However cannibalism was a serious problem and none survived later than the second instar.

Results.

The actual weights, and cumulative totals of eggs laid per individual are given in appendices 16 and 17. From these the following were calculated:

1) The mean weight (mgs.) of each species from different sites, calculated from the number of individuals alive on each date. (See Table 13).

2) The mean weight change (mgs.), per egg laid, due to egg laying. This was calculated from:

$$\frac{\text{(Mean wt. change per day for days when eggs were laid)} - \text{(Mean wt. change per day for days when no eggs were laid.)}}{\text{Mean no. of eggs laid per day when eggs were laid.}}$$

(See Table 14)

3) The period of time over which the eggs of each individual were laid. (See Table 15).

Analysis of Results.

Mean weights of each species from different sites on different dates.

Velia caprai and Gerris lateralis from Moorhouse weigh consistently less than their lowland counterparts, despite the fact that both received the same amount of food. This indicates that the Moorhouse individuals were smaller than those from the Durham

TABLE 13.

Species:	Velia caprai		Velia caprai		Gerris lateralis		Gerris lateralis		Gerris lacustris		Gerris lacustris		Gerris costai		Gerris odontogaster	
Site:	(Field Station)		(Moorhouse)		(Moorhouse)		(Field Station)		(Field Station		(Brasside)		(Moorhouse		(Brasside)	
	Mean wt.(mg.)	No. indivs.	Mean wt.(mg.)	No. indivs.	Mean wt.(mg.)	No. indivs.	Mean wt.(mg.)	No. indivs.	Mean wt.(mg.)	No. indivs.	Mean wt.(mg.)	No. indivs.	Mean wt.(mg.)	No. indivs.	Mean wt.(mg.)	No. indivs.
7 May	143	10	-	-	183	5	215	1	200	2	-	-	314	3	153	13
9 May	115	9	-	-	155	5	152	1	161	2	125	5	278	3	77	13
11 May	114	9	124	6	157	5	134	1	152	2	137	5	283	3	89	12
14 May	127	9	116	6	120	5	145	1	163	2	97	5	285	3	83	12
16 May	127	9	113	6	150	4	151	1	181	2	123	5	289	3	96	12
17 May	127	9	118	6	155	4	150	1	180	2	132	5	290	3	105	12
19 May	130	9	113	6	130	4	149	1	173	2	119	4	292	3	93	12
22 May	129	9	118	6	127	2	150	1	174	2	124	4	288	3	100	12
23 May	117	9	106	6	98	2	141	1	158	2	123	3	285	3	91	12
26 May	117	9	103	6	101	1	136	1	157	1	137	3	288	3	79	12
28 May	126	9	116	6	149	1	167	1	186	1	151	3	297	3	107	12
30 May	133	9	121	6	147	1	161	1	178	1	155	3	293	3	103	12
1 June	129	9	126	6	161	1	176	1	174	1	144	3	280	3	104	12
4 June	128	9	121	6	135	1	181	1	177	1	138	3	288	3	103	11
6 June	137	9	128	6	161	1	186	1	171	1	160	3	289	3	131	11
9 June	138	9	132	6	153	1	177	1	175	1	162	3	290	2	113	11
12 June	130	9	124	6	163	1	172	1	168	1	145	3	288	2	103	9
14 June	137	9	129	6	151	1	166	1	170	1	147	3			126	9
24 June	124	9	129	6	138	1	139	1			135	3			101	7
7 July	126	9	125	6			154	1			133	2			105	3
12 July	146	9	123	5			137	1							92	1
20 July	-	-	-	-											104	1

Mean weight in mgs. (when kept in jars) of each species from different sites.

TABLE 14. Mean weight changes (mg.) (when kept in jars) for species from different sites, in relation to egg-laying.

Species: / Site:	*Gerris lateralis* (Moorhouse)	*Gerris lateralis* (Field Station)	*Gerris lacustris* (Field Station)	*Gerris lacustris* (Brasside)	*Gerris costai* (Moorhouse)	*Gerris odontogaster* (Brasside)
a) Mean weight change (mgs.) per day for days when no eggs were laid.	-0.20	-0.20	-1.44	-0.08	-0.50	+0.87
b) Mean weight change (mgs.) per day for days when eggs were laid.	-3.40	-1.90	-1.93	-0.46	-8.68	-6.27
c) Mean weight change (mgs.) due to egg laying per day when eggs were laid. (b-a)	-3.20	-1.70	-0.49	-0.38	-8.18	-7.14
d) Mean no. eggs laid per day when eggs were laid.	3.0	2.3	3.5	1.9	5.0	1.6
e) Mean weight change (mgs.), per egg laid, due to egg-laying. (c/d).	-1.10	-0.70	-0.14	-0.20	-1.64	-4.58

TABLE 15. Period of time (days) over which eggs were laid by individual females kept in jars.

Species, site and individual no.		Period of time (days)
Gerris lateralis (Moorhouse)	(1)	-
	(2)	10
	(3)	2
	(4)	16
	(5)	12
Gerris lateralist (Durham Field Station)	(1)	17
Gerris lacustris (Durham Field Station)	(1)	-
	(2)	17
Gerris lacustris (Brasside)	(1)	17
	(2)	-
	(3)	12
	(4)	7
	(5)	10
Gerris costai (Moorhouse)	(1)	7
	(2)	-
	(3)	4
Gerris odontogaster (Brasside)	(1)	-
	(2)	-
	(3)	12
	(4)	19
	(5)	-
	(6)	-
	(7)	25
	(8)	16
	(9)	12
	(10)	19
	(11)	19
	(12)	-
	(13)	15

area. Both groups of Velia caprai show a gradual increase in weight during the experiment, probably due to the development of eggs, none of which were laid.

Period of time over which eggs were laid. (See also Appendix 17).

Unfortunately it was not possible to ensure that the individuals brought in for this experiment had not already laid eggs in the field, so only a minimum period was obtained for each individual, hence the figures vary considerably within each species. The results as a whole show that under the conditions prevailing in this experiment the eggs are not laid in batches, but laying is spread out over several weeks. G. lacustris and G. odontogaster laid two series of eggs each, concurring with the findings of previous authors. For G. lacustris, two of the four individuals which survived to the second egg-laying showed an appreciable time gap (at least 19 days) between the two series; these were the Brasside individuals nos. 1 and 5. For the Durham Field Station individual no.1 and Brasside individual no.2 the distinction between series of eggs was not so obvious. For G. odontogaster, out of 10 individuals surviving to the second series of egg laying, five (nos. 1, 3, 5, 8, and 13) showed an appreciable time gap in between (at least 14 days). However in G. odontogaster there was more overlap in time between the two series of egg-laying than in G. lacustris.

None of the Velia caprai laid their eggs during the experiment, and when they were dissected afterwards, all were found to contain large numbers of mature eggs. This is somewhat surprising since Southwood and Leston record them as laying eggs during May and early June, on moss. It must be concluded that they found the experimental conditions unsuitable for egg-laying.

The results indicate that in general the rate of egg-laying of a species is approximately proportional to the average weight of the species and inversely proportional to the mean weight lost per egg. Also a tentative suggestion may be made that the rate of egg-laying is related to extremity of environmental conditions; the Moorhouse individuals lay their eggs faster and finish laying earlier than those at Brasside, which in turn lay their eggs faster and finish laying earlier than those at Durham Field Station (the least exposed site). This would tend to counteract the longer time of development of eggs and larvae at lower temperatures.

GENERAL DISCUSSION.

The theorem attributed to Gause, that "two species with the same ecology cannot co-exist," has provoked much controversy amongst ecologists. This is chiefly because of difficulties in defining words such as "same", "ecology", and "co-exist"; however the fundamental idea behind it has given stimulus and direction to research for many years. It may be applied to the present situation in the following form: closely related surface-dwelling water bugs can share the same pond provided their ecological requirements differ in some aspect. A few conclusions may be drawn from this study concerning the factors which delimit the habitat of each species, and which affect the ecology of the group as a whole. The study also suggests several possible lines for further investigation.

In many animals food is the chief resource limiting both their habitat and population numbers. This study gives a comparison of the amount of potential food on several lowland ponds at Brasside, and on upland pond at Moorhouse. The maximum density of gerrids on the Moorhouse pond was $1.3/m^2$, a figure similar in magnitude to most of the Brasside ponds ($0.62 - 2.46/m^2$). However the potential food at Moorhouse was less than a third that of most Brasside ponds; hence it may be concluded that at Brasside, and probably similar lowland sites, potential food was in excess and not a limiting factor.

However the availability of the food to gerrids may be limited by characteristics of the pond; for example it was found that Potamogeton natans may hinder gerrids in their hunting by slowing them down, and making escape easier for the prey. The food requirements of the different species of gerrids were not considered in this study, but might

possibly constitute a difference in ecological requirements sufficient to allow coexistence on the same pond.

Climate undoubtedly plays an important role in the ecology of Gerris and Velia species. The build up of numbers of gerrids after overwintering, the gradual increase in mortality during the season, and the rise in numbers as the new generation of adults appears to follow a similar cycle at Moorhouse and Brasside, however everything occurs about a fortnight later at Brasside than at Moorhouse. If the rate of egg-laying of gerrids is inversely proportional to the percentage of weight lost for each egg laid, and if the individuals at Moorhouse are smaller, and lay their eggs more quickly than their lowland counterparts, this places another restriction on the ecology of species inhabiting the more extreme environment. G. costai seems to be best adapted to these restrictions; hence it is not surprising that it is the only purely upland species of Gerris.

The importance of vegetation may be connected with its prevention of wave-formation on ponds. Waves could be prevented from forming either by standing vegetation or floating vegetation. Floating vegetation such as Ricciocarpus natans and Lemna trisulca is tolerated by gerrids, and also sparsely distributed Potamogeton natans. However, standing vegetation also provides shelter from rain. G. costai deserted Greenhole pond which had no standing vegetation at all. This study also suggests that G.lacustris has a preference for water where the standing vegetation is not too closely packed. G. lacustris was the only species observed around the shores of the three lakes at Brasside; the vegetation here consisted chiefly of sparsely distributed Typha latifolia, and no floating vegetation. Possibly

G. lacustris can tolerate greater disturbance of the surface than G. odontogaster. Further experimental work would clarify this.

The life cycles of the various species of Gerris and Velia all differ slightly, so that even if their food requirements are similar the period of maximum pressure on food resources varies between species. G. odontogaster and G. lacustris, which seem to have very similar ecology in many aspects, and both have two generations a year, differ slightly in the time of appearance of the first new generation, G. lacustris appearing about a fortnight later than G. odontogaster. Brinkhurst (1966) suggests that a major cause of the spring-autumn mortality in G. najas is cannibalism among the nymphs. An interesting line for further investigation would be the interaction of nymphs of G. odontogaster and G. lacustris in mixed populations.

Velia caprai has often been observed on the same ponds and streams as G. lateralis and G. lacustris. A difference in ecology noted in this study is that since Velia did not lay any eggs when kept in jars, whereas all species of Gerris studied did lay eggs, they obviously have different requirements in egg-laying sites. Also since Velia move more slowly than Gerris, one would expect them to be at a disadvantage when competing with Gerris for food in large areas of water; this could be a factor restricting them to streams and small ponds, and would make interesting further investigation.

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Note on Appendices 1-4: Individual captures in the ponds on successive dates.

A cross + indicates the individual was captured on that day; a cross in brackets (+) indicates the individual was not captured but previous and subsequent captures suggest that it almost certainly was present on that date. The 'total present' row includes those crossed in brackets. 'Proportions caught' are estimated from the number captured divided by the number thought to be present. Numbers gained are those individuals not captured in the pond before; numbers lost are those which are not present on the given date, which were present the previous date, and were never captured again during the experiment. An unavoidable error in this method of interpreting the data is that since some individuals were missed each time, they may be regarded as gains or losses before or after being gained or lost from the pond; however since these errors occur in both directions they almost certainly tend to cancel each other out. The 'comments' row indicates when it was raining during the collection, or periods when it was very dry.

APPENDIX 1. Individual captures on pond E on successive dates.

Species and individuals.	Date. 21/5	25/5	31/5	10/6	18/6	27/6	12/7	19/7	29/7	30/7	5/8
G. lacustris											
1	+	+	+	+							
2	+	+	+								
3	+	+	+								
4	+	+	+	+	(+)	+					
5	+										
6	+	+	+								
7	+	+	+	+							
8	+	+	+								
9		+	(+)	+							
10			+								
11			+	+	(+)	+					
12			+								
13										+	+
14											+
15											+
Total present	8	8	11	5	2	2	0	0	0	1	3
Proportion caught	1.0	1.0	0.9	1.0	0.0	1.0	1.0	1.0	1.0	1.0	1.0
G. odontogaster											
1	+	+	+	+							
2	+	+	+								
3	+	+									
4		+	+								
Total present	3	4	3	1	0	0	0	0	0	0	0
Proportion caught	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Appendix 1 (Cont'd).

Species and individuals.	21/5	25/5	31/5	10/6	18/6	27/6	12/7	19/7	29/7	30/7	5/8
G. thoracicus											
1	+	+									
Total present	1	1									
Proportion caught	1.0	1.0									
G. lateralis											
1		+	(+)	+	(+)	+					
2			+								
3									+		
4									+		
Total present	0	1	2	1	1	1	0	0	2		
Proportion caught	1.0	1.0	0.5	1.0	0.0	1.0	1.0	1.0	1.0		
Total for all species	12	14	16	7	3	3	0	0	2	1	3
Proportion caught for all species	1.0	1.0	0.9	1.0	0.0	1.0	1.0	1.0	1.0	1.0	1.0
Comments:					Raining		Very dry	Very dry			

All individuals for all species were macropterous.

APPENDIX 2. Individual captures on pond F on successive dates

Species and individuals	Date 28/4	3/5	12/5	18/5	25/5	1/6	9/6	18/6	24/6	12/7	19/7	29/7	5/8
G. lacustris													
1	+												
2(	+	+	(+)	+	+	+							
3	+	+	+	+	+	+	+	+	+				
4		+	+	+	+	+	+						
5			+	+	+	(+)	+						
6			+	+	+	+	+	+	+				
7			+	+	+								
8			+	+									
9			+	+									
10				+	+	(+)	+						
11				+	+	+	+	(+)	+				
12						+	+						
13						+							
Total present	3	3	8	10	8	9	7	3	3				
Proportion caught	1.0	1.0	0.9	1.0	1.0	0.8	1.0	0.7	1.0				
G. odontogaster													
1	+	+	(+)	(+)	+	+	+						
2	+	+	(+)	+	+	+							
3	+	+	(+)	(+)	+	+	+	(+)	+				
4	+	+	+	+	+	(+)	+	(+)	+				
5		+	+	+	(+)	+	+	+	+				
6		+	(+)	+									

APPENDIX 2 (Cont'd)

G. odontogaster (cont'd)	28/4	3/5	12/5	18/5	25/5	1/6	9/6	18/6	24/6	12/7	19/7	24/7	5/8
7			+	+	(+)	+							
8			+	+	+								
9			+	(+)	+								
10				+	+	+	+	(+)	+				
11				+	+	+							
12					+	+	(+)	+					
13						+							
14									+				
15									+				
16												+	+
17												+	
18												+	
19												+	
20												+	+
21												+	
22													+
23													+
24													+
25													+
26													+
27													+
28													+
Total present	4	6	9	11	11	10	6	5	6	0	0	6	9
Proportion caught	1.0	1.0	0.6	0.7	0.8	0.9	0.8	0.4	1.0	1.0	1.0	1.0	1.0

APPENDIX 2 (Cont'd)

Species and individuals	Date 28/4	3/5	12/5	18/5	25/5	1/6	9/6	18/6	24/6	12/7	19/7	29/7	5/8
G. thoracicus			+										
1			+										
2			+	+	+								
Total present	0	0	2	1	1	0	0	0	0	0	0	0	0
Proportion caught	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
G. lateralis													
1												+	
Total present	0	0	0	0	0	0	0	0	0	0	0	1	0
Proportion caught	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Total for all species	7	9	19	22	20	19	13	8	9	0	0	7	9
Proportion caught for all species	1.0	1.0	0.7	0.9	0.9	0.8	0.9	0.5	1.0	1.0	1.0	1.0	1.0
Comments:								Rain-ing		Very dry	Very dry		

All individuals (except G. lacustris no.2) of all species were macropterous.

APPENDIX 3. Individual captures on Bog End pond on successive dates.

Species and individuals	Date 11/5	17/5	26/5	2/6	8/6	25/6	1/7	8/7	13/7	20/7	28/7	3/8
G. costai												
1 (from Greenhole)	+	+	+	+	+							
2	+	(+)	+	+	+							
3	+											
4	+	(+)	+	+	+	(+)	+	+	+	+		
5		+	+	+	+	+						
6				+	(+)	+						
Total present	4	4	4	5	5	3	1	1	1	1	0	0
Proportion caught	1.0	0.5	1.0	1.0	0.8	0.7	1.0	1.0	1.0	1.0	1.0	1.0
G. lateralis												
1	+	(+)	+									
2	+	+	+									
3	+	(+)	+	+								
4	+	+	+.	+								
5	+	+										
6	+	(+)	+	+	+	+						
7	+	(+)	+	+	+							
8	+	(+)	+									
9	+	+	+	+	+	+	(+)	+				
10	+	(+)	+									
11	+	(+)	+	+	+	(+)	+	+				
12	+	(+)	(+)	+								
13	+	+	+	+	+	+						

APPENDIX 3 (Cont'd)

G. lateralis	11/5	17/5	26/5	2/6	8/6	25/6	1/7	8/7	13/7	20/7	28/7	3/8
14			+	(+)	+	+						
15			+	+	+	(+)	+	(+)	+	(+)	+	
16			+	(+)	+							
17			+	(+)	+							
18				+	+							
19				+	+							
20				+	+	(+)	+	(+)	(+)	(+)	+	+
21				+	+	(+)	(+)	+				
22							+	(+)	(+)	+	+	
23												+
24												+
25												+
26												+
27												+
Total present	13	13	16	16	14	8	6	6	3	3	3	6
Proportion caught	1.0	0.4	0.9	0.8	1.0	0.5	0.7	0.5	0.3	0.3	1.0	1.0
Total for both species	17	17	20	21	19	11	7	7	4	4	3	6
Proportion caught for both species		0.5	0.9	0.9	0.9	0.6	0.7	0.6	0.5	0.5	1.0	1.0
Comments:		Rain-ing				Rain-ing			Very dry	Very dry		

All individuals of G. costai were macropterous and all individuals of G. lateralis were apterous.

APPENDIX 4. Individual captures on Greenhole pond on successive dates.

Species and individuals	Date 21/4	29/4	5/5	11/5	17/5	26/5	2/6	8/6	25/6	1/7	8/7	13/7	20/7	28/7	3/8
G. costai															
1	+	+													
2	+	+													
3	+	+	+	+	+										
4	+	(+)	+	+	+										
5	+	+	+	+											
6	+	+													
7	+														
8	+	+	On Bog End pond												
9	+	+	+	+	+										
10	+	+	+	+											
11	+	+	+	+	+										
12	+	+													
13	+	+	+	+	+										
14	+	+													
15				+											
16					+										
Total present	14	13	7	8	6	0	0	0	0	0	0	0	0	0	0
Proportion caught	1.0	0.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Comments:		Raining			Raining				Raining			Very dry	Very dry		

All individuals of G. costai were macropterous.

APPENDIX 5.

Values of a_1, a_2, n_3, r_{21}, r_{31}, and r_{32} for each pond on which the population was estimated by the Lincoln index method.

	$a_1 (=n_1)$	$a_2 (=n_2)$	n_3	r_{21}	r_{31}	r_{32}
Pond A	30	23	37	12	20	19
B	33	28	56	11	16	16
G	15	19	7	9	2	6

a_1 = the total number of marked animals released on the first day.

a_2 = the total number of marked animals released on the second day.

n_1 = the total number of animals captured on the first day.

n_2 = the total number of animals captured on the second day.

n_3 = the total number of animals captured on the third day.

r = recaptures, the first subscript representing the day of captures and the second the day of marking.

APPENDIX 6.

Numbers of marked and unmarked Velia captured at Durham Field Station stream.

Sites :	(1)		(2)		(3)		(4)		(5)	
Dates	MARK.	UNM.	MARK.	UNM.	MARK.	UNM.	MARK.	UNM.	MARK.	UNM.
2 Feb.				2						
2 March				1						
30 March		13		29		14		6		
16 April	1	35	4	9	2	15	0	13		7
22 April	1	23	1	18	2	13	0	10	0	22
4 May	9	92	3	11	4	12			0	7
12 May	15	23	2	11	6	10			2	20
19 May	23	26	12	24	0	3	1	9	0	26
27 May	9	13	2	11	0	0	1	9	0	7

APPENDIX 7.

Values of a, r, and n for each site on different dates (see text).

	(1)			(2)			(3)			(4)			(5)		
	a	r	n	a	r	n	a	r	n	a	r	n	a	r	n
30 Mar.	0		13	3		29	0		14	0		6			
16 Apr.	13	1	36	32	4	13	14	2	17	6	0	13			7
22 Apr.	48	1	24	41	1	19	29	2	15	19	0	10	7	0	22
4 May	71	9	101	59	3	14	42	4	16	29			29	0	7
12 May	163	15	38	70	2	13	54	6	16	29			36	2	22
19 May	186	23	49	81	12	36	64	0	3	29	1	10	56	0	26
27 May	212	9	22	105	2	13	67	0	0	38	1	10	82	0	7

APPENDIX 7. Foodtraps - results of 8-hourly collections.

Ponds, dates and times	Orders: ODONATA	TRICHOPTERA	DIPTERA	HYMENOPTERA	COLEOPTERA	PSOCOPTERA	HEMIPTERA	THYSANOPTERA	COLLEMBOLA	ARACHNIDA
POND A 29/6 8.00 hrs.			9							
16.00 "			25	1						
24.00 "	(		2							)
30/6 8.00 "			5							
16.00 "			4							1
24.00 "	(		2							)
POND B 29/6 8.00 hrs.			2							1
16.00			6	1						
24.00			4							
30/6 8.00			5							1
16.00			2				1	1		
24.00			2		1		1			
POND C 29/6 8.00 hrs.			3		1					
16.00			7							1
24.00	(		2							)
30/6 8.00			7							
16.00		2	19				1			
24.00			1							
POND D 29/6 8.00 hrs.		1	3							
16.00			1							
24.00	(		1							)
30/6 8.00	(	1	3							)
16.00			3							
24.00			1							
POND E 29/6 8.00 hrs.			5			1				
16.00		1	5							
24.00			1							
30/6 8.00			9		1		1		2	
16.00			4	3			1			
24.00	(		1							)
POND F 24/6 8.00 hrs.			3		1					
16.00			2		1			1		
24.00	(		1							)
30/6 8.00			3							
16.00	2		2				1			
24.00	(		1							)

APPENDIX 8. Foodtraps - results of weekly collections.

Ponds, dates and veg./ non-veg.	ODONATA	TRICHOPTERA	DIPTERA	HYMENOPTERA	COLEOPTERA	PSOCOPTERA	HEMIPTERA	THYSANOPTERA	COLLEMBOLA	ARACHNIDA
POND A										
28/6 VEG		2	116	3						
NON-VEG		1	37	4			2			
12/7 V	(	3	89	3						)
N	(	1	53	3			2			)
19/7 V	(	4	89	3						)
N	(	2	54	3			4			1)
25/7 V		5	62	3						
N		2	70	2						1
POND B										
28/6 V		1	37	1						
N		1	95							
12/7 V		1	37	1						
N		1	95							
19/7 V		1	37	1						
N		1	95							
25/7 V		1	37	1						
N		1	95							
POND C										
28/6 V	1	5	78	1						
N		8	122	1	2					
12/7 V	1	1	54	3			2			
N	1	3	60	1	4		1			
19/7 V	1	2	84							
N		5	116	1	1		2			
25/7 V	1	4	50	1		2	2	1		
N		1	60							
MOOR-HOUSE POND										
25/7 each			31							
side			31							

Ponds, dates and veg./ non-veg.	ODONATA	TRICHOPTERA	DIPTERA	HYMENOPTERA	COLEOPTERA	PSOCOPTERA	HEMIPTERA	THYSANOPTERA	COLLEMBOLA	ARACHNIDA
POND D										
28/6 VEG		2	62	1						
NON-VEG	4	1	70	1	6					
12/7 V	6	1	64	1	1					
N	1	1	50		2		2			
19/7 V			132		8					
N	4	1	52	3	4	1				
25/7 V	(2	1	86	1	3					
N	(3	1	57	1	4		1			
POND E										
28/6 V	2	3	92							
N	1	4	116	1	2					
12/7 V		3	74		2				4	
N	(2	1	87		5					
19/7 V	1	1	114	1	2					
N	4		52		2		1			1
25/7 V			98	2			4			
N			94		10					
POND F										
28/6 V		1	150	2			1			
N	1	2	162	1						
12/7 V	1		91		1					
N	3	5	97	1	1					4
19/7 V			148							
N	3		126	4						
25/7 V		1	60		2					
N	1	2	48							

Dates indicate the end of each 7-day period.

APPENDIX 9. Total numbers of individuals trapped in different orders for all ponds at various times of day.

Orders	Time collected (hrs.) 8.00	16.00	24.00	Total
ODONATA	0	2	0	2
TRICHOPTERA	2	5	0	7
DIPTERA	57	80	19	156
HYMENOPTERA	0	5	0	5
COLEOPTERA	3	1	1	5
PSOCOPTERA	1	0	0	1
HEMIPTERA	1	4	1	6
THYSANOPTERA	0	2	0	2
COLLEMBOLA	2	0	0	2
ARACHNIDA	2	2	0	4
Total	68	101	21	190

Null Hypothesis: that there is no significant difference between totals.

Totals tested	χ^2	Degrees of freedom.	P
Totals for different time periods	51.05	2	Less than .001
For Diptera only at different time periods	36.50	2	Less than .001
For all other orders at different time periods	16.02	2	Less than .001

The Null Hypothesis may be rejected at the 0.1% level of probability in all cases, and there is a significant difference between the overall totals, between the totals for Diptera, and between the totals for all other orders at different time periods. It is seen from the table that the total food for all ponds together was at a peak between 8.00 and 16.00 hrs., and at a minimum between 16.00 and 24.00 hrs. This pattern also occurs in the numbers of Diptera, and for all the other orders together.

APPENDIX 10. Total numbers of individuals trapped at various times of day on different ponds.

Time collected (hrs.)	A	B	C	D	E	F	Total
8.00	14	9	11	8	19	7	68
16.00	32	12	30	4	14	9	101
24.00	4	8	3	2	2	2	21
Total	50	29	44	14	35	18	190

Null Hypothesis: that there is no significant difference between totals.

Totals at different times for ponds	χ^2	Degrees of freedom	P
A	24.1	2	Less than .001
B	0.9	2	Not significant
C	26.2	2	Less than .001
D	4.0	2	Not significant
E	13.1	2	Less than .01
F	4.3	2	Not significant

The Null Hypothesis must be accepted for ponds B, D and F. For pond E the Null Hypothesis may be rejected at the 1% level, and for ponds A and C at the 0.1% probability level.

Percentages of the total for each pond at different times.

Time collected (hrs.)	A	B	C	D	E	F
8.00	28.0	31.0	25.0	57.1	54.3	38.9
16.00	64.0	41.4	68.2	28.6	40.0	50.0
24.00	8.0	27.6	6.8	14.3	5.7	11.1

Clearly the amount of food is less between 16.00 and 24.00 hours than for either of the other 8 hourly periods; for ponds A and C there is more food coming in between 8.00 and 16.00 hrs than between 24.00 and 8.00 hrs. For ponds B, D, F, longer samples would probably have resulted in a significant difference between totals at different times, and might have clarified the time period of maximum amount of food coming into the ponds.

APPENDIX 11. Total numbers of individuals trapped for different weekly periods on each pond.

Date	Ponds. A	B	C	D	E	F	Total
28 June	163	135	218	147	221	320	1204
12 July	154	135	131	129	178	204	931
19 July	158	135	212	205	179	281	1170
25 July	149	135	122	160	208	114	888
Total	624	540	683	641	782	919	4193

Null Hypothesis: that there is no significant difference between totals.

Totals tested	χ^2	Degrees of freedom	P
Totals for different date	75.9	3	Less than .001
Totals for different ponds	129.0	5	Less than .001

The Null Hypothesis may be rejected in both cases, there is a significant difference between totals on different dates and between totals for different ponds.

Percentages of total per weekly period for the different ponds.

Date	Ponds A	B	C	D	E	F
28 June	13.5	11.2	17.5	12.2	18.4	26.6
12 July	16.5	14.5	14.1	13.9	19.1	21.9
19 July	13.5	11.5	18.1	17.5	15.3	24.0
25 July	16.8	15.2	13.7	18.0	23.4	12.8

These percentages indicate that the relative proportions of food on different ponds were approximately similar in the different weekly collections.

APPENDIX 12. Total numbers of individuals trapped for various orders on different ponds.

Orders	Ponds. A	B	C	D	E	F	Total
ODONATA	0	0	5	20	10	9	44
TRICHOPTERA	20	8	29	8	12	11	88
DIPTERA	270	528	624	573	727	882	3904
HYMENOPTERA	24	4	8	8	4	8	56
COLEOPTERA	0	0	7	28	23	4	62
HEMIPTERA	8	0	7	3	5	1	24
THYSANOPTERA	0	0	1	0	0	0	1
COLLEMBOLA	0	0	0	0	4	0	4
PSOCOPTERA	0	0	2	1	0	0	3
ARACHNIDA	2	0	0	0	1	4	7
Total	624	540	683	641	786	919	4193

Percentages of the total per pond from each order.

Orders	Ponds. A	B	C	D	E	F
ODONATA	0	0	0.7	3.1	1.3	1.0
TRICHOPTERA	3.2	1.5	4.0	1.2	1.5	1.2
DIPTERA	91.3	97.8	91.4	89.4	92.5	96.0
HYMENOPTERA	3.8	0.7	1.2	1.2	0.5	0.9
COLEOPTERA	0	0	1.0	4.4	2.9	0.4
HEMIPTERA	1.3	0	1.0	0.5	0.6	0.1
THYSANOPTERA	0	0	0.1	0	0	0
COLLEMBOLA	0	0	0	0	0.5	0
PSOCOPTERA	0	0	0.3	0.2	0	0
ARACHNIDA	0.3	0	0	0	0.1	0.4

The percentages indicate that the relative composition of the food on different ponds was very similar with regard to orders of animals present.

APPENDIX 13. Total numbers of individuals trapped for various orders on different dates.

Orders	Date 28/7	12/7	19/7	25/7	Total
ODONATA	9	15	13	7	44
TRICHOPTERA	31	21	17	19	88
DIPTERA	1137	851	1099	817	3904
HYMENOPETRA	16	13	16	11	56
COLEOPTERA	10	16	17	19	62
PSOCOPTERA	0	0	1	2	3
HEMIPTERA	1	7	5	11	24
THYSANOPTERA	0	0	0	1	1
COLLEMBOLA	0	4	0	0	4
ARACHNIDA	0	4	2	1	7

Percentages of totals per week in different orders.

Orders	Date 28/7	12/7	19/7	25/7
ODONATA	0.7	1.6	1.1	0.8
TRICHOPTERA	2.6	2.3	1.5	2.1
DIPTERA	94.4	91.4	93.9	93.0
HYMENOPETRA	1.3	1.4	1.4	1.2
COLEOPTERA	0.8	1.7	1.5	2.1
PSOCOPTERA	0	0	0.1	0.2
HEMIPTERA	0.1	0.8	0.4	1.2
THYSONOPTERA	0	0	0	0.1
COLLEMBOLA	0	0.4	0	0
ARACHNIDA	0	0.4	0.2	0.1

The percentages show that the composition of food with regard to the orders present was very similar on the different weeks.

APPENDIX 14. Total numbers of individual in different orders on the veg. and non-veg. sides of the traps.

Numbers for each order

Orders	Veg.	Non-veg.
ODONATA	16	28
TRICHOPTERA	43	45
DIPTERA	1941	1963
HYMENOPTERA	29	27
COLEOPTERA	19	43
HEMIPTERA	17	7
THYSANOPTERA	1	0
COLLEMBOLA	4	0
PSOCOPTERA	0	1
ARACHNIDA	0	7
Total	2072	2121

Percentages

Orders	Veg.	Non-veg.
ODONATA	47	53
TRICHOPTERA	49	51
DIPTERA	50	50
HYMENOPTERA	52	48
COLEOPTERA	31	69
HEMIPTERA	71	29
THYSONOPTERA	100	0
COLLEMBOLA	100	0
PSOCOPTERA	0	100
ARACHNIDA	0	100

Null Hypothesis: that there is no significant difference between totals.

Totals tested	χ^2	Degrees of freedom	P
ODONATA	3.27	1	Not significant
TRICHOPTERA	0.04	1	Not significant
DIPTERA	0.12	1	Not significant
HYMENOPTERA	0.07	1	Not significant
COLEOPTERA	9.29	1	Less than .01
HEMIPTERA	2.53	1	Not significant

The Null Hypothesis must be accepted for all orders tested except Coleoptera, which has a significant difference between the veg. and non-veg. sides of the trap at the 1% level of probability.

APPENDIX 15. Total numbers trapped on the veg. and non-veg. sides of the traps on different ponds.

	Ponds A	B	C	D	E	F	Total
Veg.	390	156	294	371	403	458	2072
Non-veg.	234	384	389	270	383	461	2121
Total	624	540	683	641	786	919	4193

Null Hypothesis: that there is no significant difference in the totals for veg. and non-veg. on different ponds.

Pond totals tested	χ^2	Degrees of freedom	P
A	39.00	1	Less than .001
B	96.30	1	Less than .001
C	13.21	1	Less than .001
D	15.91	1	Less than .001
E	2.70	1	Not significant
F	0.01	1	Not significant

The Null Hypothesis may be rejected for ponds A, B, C and D, and there is a significant difference between the totals for veg. and non-veg. on these ponds, though from the table it is seen that for ponds B and C the non-veg. side had higher numbers, while for ponds A and D the veg. side of the trap had higher numbers of individuals. The Null Hypothesis must be accepted for ponds E and F.

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APPENDIX 16. Weights in mgs. of individual females on successive dates (kept in jars).

Species, site and individual no.	Date	7/5	9/5	11/5	14/5	16/5	17/5	19/5	22/5	23/5	26/5	28/5	30/5	1/6	4/6	6/6	9/6	12/6	14/6	24/6	7/7	12/7	20/7
Velia caprai (Moorhouse)	1)	-	-	121	118	115	116	113	120	105	102	117	123	125	120	125	131	126	132	134	129	127	-
	2)	-	-	120	111	110	116	112	120	107	104	119	121	125	116	129	129	126	131	130	122	-	-
	3)	-	-	132	121	118	122	117	123	109	109	121	127	131	127	134	138	129	131	128	126	124	-
	4)	-	-	114	107	105	117	109	110	100	96	108	111	115	109	114	121	114	117	116	113	113	-
	5)	-	-	128	119	116	119	114	120	109	104	116	124	131	131	130	137	122	131	133	129	126	-
	6)	-	-	126	119	116	119	115	117	104	104	116	120	126	122	137	137	127	131	131	128	126	-
Velia caprai (Durham Field Station)	1)	147	120	116	124	123	130	124	117	120	128	137	133	123	137	135	125	127	115	121	131	-	-
	2)	142	117	121	132	131	137	135	126	130	137	141	141	140	149	148	147	146	138	141	144	-	-
	3)	140	109	112	127	122	123	129	117	111	128	133	124	129	134	135	132	140	124	126	162	-	-
	4)	152	116	117	132	129	133	138	120	121	121	130	126	129	137	138	131	131	118	126	151	-	-
	5)	141	115	114	131	122	128	127	115	112	123	130	126	124	135	135	120	123	114	116	144	-	-
	6)	150	115	116	124	132	138	133	121	120	124	133	131	130	141	144	136	139	125	135	156	-	-
	7)	133																					
	8)	138	113	108	124	127	127	125	112	114	124	130	126	126	132	134	126	146	120	120	140	-	-
	9)	149	123	114	130	136	133	132	118	123	133	135	134	136	141	141	132	146	139	128	147	-	-
	10)	137	103	106	121	118	118	116	109	104	120	126	122	119	130	135	124	138	123	120	136	-	-
Gerris lateralis (Moorhouse)	1)	202	197	208																			
	2)	169	157	152	135	160	156	136															
	3)	173	128	136	105	143	148	136	132	105													
	4)	165	127	134	100	134	146	119	122	91	101	149	147	161	135	161	156	163	151	138	-	-	-
	5)	204	164	157	138	161	170																
G.lateralis (Durham Field Station)	1)	215	152	134	145	151	150	149	150	141	136	167	161	176	181	186	177	172	166	139	154	137	-
G.lacustris (Durham Field Station	1)	182	141	146	160	175	176	168	170	153	157	186	178	174	177	171	175	168	170				
	2)	217	181	157	166	186	184	177	177	163													
G.lacustris (Brasside)	1)	152	159	104	132	139	126	133	127	109	148	149	135	128	145	140	135	137	133	136	-	-	-
	2)	95	119	91	123	139	118	117	109	137	127	135	129	119	140	146	135	137	133	-	-	-	-
	3)	117	130	86	107	110	96	110															
	4)	100	123	84	109	114																	
	5)	162	153	120	144	159	136	137	133	165	178	182	167	167	195	200	165	166	139	130	-	-	-
G. costai (Moorhouse)	1)	323	288	333	310	307	321	313	311	304	317	315	315	293	301	313	322	299					
	2)	283	248	251	270	274	279	280	269	264	273	285	280	280	271	263	237						
	3)	335	297	266	275	286	271	284	283	286	273	292	285	267	293	292	312	276					
G. odontogaster (Brasside)	1)	147	86	91	85	99	114	106	113	106	95	114	120	111									
	2)	149	94	100	92	104	112	88	100	91	82	103	105	104	101	110	108	101	114	103	-	-	-
	3)	154	74	90	76	90	100	86	100	89	93	102	107	108	104	127	115	108	114	100	-	-	-
	4)	150	78	90	89	97	112	99	108	101	83	106	107	108	104	124	121	108	118	102	-	-	-
	5)	141	71	78	75	84	102	92	102	95	81	109	105	108	107	122	112	103	111	95	112	-	-
	6)	151	71	87	82	97	104	92	98	92	79	109	102	108	103	122	114	103	111	95	115	-	-
	7)	155	72	91	90	95	102	96	98	85	73	109	99	96	94	116	114	106	117	110	88	92	104
	8)	165	77	86	80	96	102	93	98	86	79	108	100	110	103	120	111	100	114	101			
	9)	150	70	87	80	98	102	92	97	87	72	107	98	93	105	114	110						

APPENDIX 17. Cumulative numbers of eggs laid by individual females on successive dates (kept in jars).

Species, site and individual no.		7/5	9/5	11/5	14/5	16/5	17/5	19/5	22/5	23/5	26/5	28/5	30/5	1/6	4/6	6/6	9/6	12/6	14/6	24/6	7/7	12/7	20/7
Gerris lateralis (Moorhouse)	(1)	0	0	0	0																		
	(2)	0	0	12	13	13	16	25	25														
	(3)	0	0	6	6	6	6	6	6	6	6												
	(4)	0	14	14	16	17	17	24	28	29	29	29	29	29	29	29	29	41	57	78			
	(5)	0	3	13	13	13	13	25															
G.lateralis (Durham Field Station)	(1)	0	0	23	31	32	32	36	39	39	40	40	40	40	40	40	52	55	61	77	77	77	
G.lacustris (Durham Field Station)	(1)	0	0	0	0	0	0	0	0	0	8	8	8	15	15	23	23	23	23	23			
	(2)	0	0	19	19	19	19	19	29	29	30												
G.lacustris (Brasside)	(1)	0	0	11	15	15	15	15	16	16	17	17	17	17	17	17	17	17	20	20			
	(2)	0	0	0	0	3	3	6	6	6	7	8	8	9	9	9	16	18	18	18			
	(3)	0	10	21	26	28	28	29	29														
	(4)	0	7	13	16	16	16																
	(5)	0	20	20	20	21	27	27	27	27	27	27	27	27	27	27	27	32	42				
G. costai (Moorhouse)	(1)	0	2	23	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35				
	(2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
	(3)	0	0	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10				
G. odontogaster (Brasside)	(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	3								
	(2)	0	0	0	0	0	0	15	16	16	16	16	16	17	19	19	19	19	19	36	36		
	(3)	0	0	0	4	6	7	7	7	8	8	8	8	8	8	8	12	17	17	22	22		
	(4)	0	1	1	1	1	1	1	5	5	7	7	7	7	9	10	10	14	17	35	35		
	(5)	00	0	0	0	0	0	0	0	0	0	0	0	0	0	5	11	11	12	31	31	31	
	(6)	0	4	4	4	4	4	6	6	6	6	6	7	8	8	8	8	12	22	30	30	30	
	(7)	0	6	8	8	8	14	14	17	17	18	19	19	20	20	20	20	20	23	30	43	43	43
	(8)	0	18	18	18	18	21	21	21	24	24	24	24	24	24	24	24	24	25	39	39		
	(9)	0	3	3	3	3	5	6	6	6	6	6	6	6	6	6	6	6					
	(10)	0	9	9	9	9	11	14	14	14	15	15	15	15	15	15	15	15					
	(11)	0	8	9	9	9	9	14	14	15	16	16	16	16	17	17	17	18	19	27			
	(12)	0	0	0																			
	(13)	0	10	10	10	10	13	13	15	15	15	15	15	15	15	15	15	19	19	19			

(No eggs were laid by Velia caprai from either Moorhouse or Durham Field Station during the period of study).