OBSERVATIONS ON THE DRY LAND ORIENTATION OF *GYRINUS MARINUS* GY *(CARABOIDEA: COL:)*

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It was noticed that gyrinid beetles caught in the River Stour would head back towards the river if put on the ground. Since this appeared to be an orientation behaviour unconnected with direct movement towards the sun, its mechanism seemed worth investigating. These beetles (*Gyrinus marinus* Gy.) can move on land though they appear not to be able to raise their bodies off the ground into the posture usually associated with a running beetle. However, they move quickly over smooth and rough surfaces and they can take flight from them.

Though station-keeping behaviour of the swarms of the related American *Dineutes discolor* Aubé swimming on the water surface has been studied (Brown and Hatch, 1929), orientation on land has not previously been investigated in that species or in any species of *Gyrinus*.

Methods

Beetles were netted from swarms on the water surface by the bank of a section of the River Stour near Flatford Mill. Along this stretch the river runs approximately West to East. The positions of swarms during 1959 and 1960 are shown in Fig. 1. They occupied similar positions in 1961, but were fewer

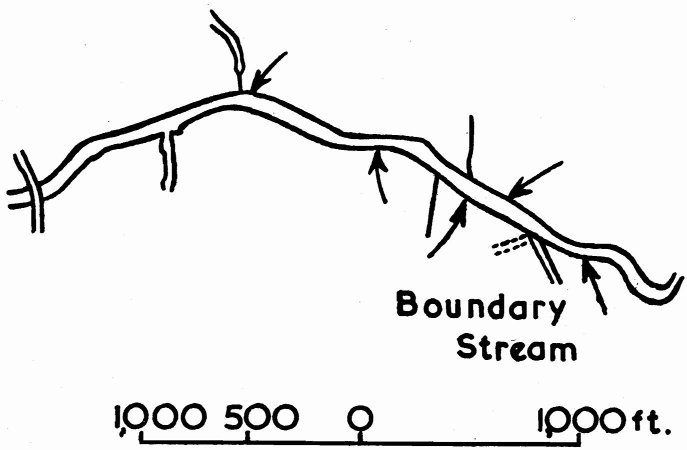

Fig. 1.
Map of the Stour, near Flatford Mill, showing position of *Gyrinus* swarms (re-drawn from 6 inch to 1 mile Ordinance Survey map).

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in 1962. Since then this beetle has not appeared on this stretch of the Stour, perhaps eliminated by the increase in pollution of the river.

In experiments in the field beetles were placed on the centre of a sheet of thin cardboard fixed to a board and carefully levelled. Pencil lines radiated from the centre to sixteen equally spaced points of the compass. The North line of this "rose" was always aligned to magnetic North. The insects were either put on the board one by one for individual tracks to be followed or numbers of beetles were released together from the centre and the points where they crossed the outer margin of the "rose" noted (massed release).

Each individual was placed in the centre of the compass rose, tracked to its edge, picked up, replaced in the centre and re-tracked. This was repeated for five successive runs. There was remarkable constancy in the directions of each one of the set of five runs of any one beetle. The directions were taken up rapidly and usually without hesitation.

Tracks could be followed on the board by drawing a pencil behind the beetle as it moved. This caused no disturbance, the results being similar to tests without following with a pencil. However, it was often more convenient to trace the tracks on a sheet of paper marked with a similar set of compass points, the overall size of the "rose" on this paper being one third that on the board.

The beetles are unstable when moving on paper so that if there was a wind they were liable to be turned over. On a few occasions it was necessary to shield them or to cover them with an inverted 3 inches by 1 inch glass specimen tube. The tube was moved along as the beetle moved so that the insect did not come into contact with the wall of the tube. This, too, did not apparently disturb the beetle's orientation. The use of a larger glass cover would be preferable.

It was possible to mark individuals with quick-drying enamel but the marks did not adhere for more than three days at the most. Generally they were lost sooner, for the dorsal surface of this beetle is very smooth.

RESULTS

Orientation of beetles from south-side swarms

The tracks of beetles placed on the compass board two feet from the bank edge are shown in Fig. 2*a*. These beetles were freshly caught from a swarm close to that bank. When transported to the north bank of the river and released individually, they headed predominantly North (Fig. 2*b*). At the time when the results shown in Fig. 2 were obtained there was a fringe of *Epilobium hirsutum* growing along the north bank between the river and the ploughed field beyond. Since the releases were made in the field close to this screen it is most unlikely that the beetles could have seen any of the landmarks, e.g. trees, on the south bank. It may be noted that when the same beetles were released on the water surface they headed southwards across the river, reversing the direction of their dry-land orientation. It can be seen from Fig. 2 that the initial heading of a beetle did not influence its subsequent path for correcting movements were made to bring it to the preferred final heading. Although as a precaution beetles were released individually there was at no time any evidence of one following another; each orientated independently.

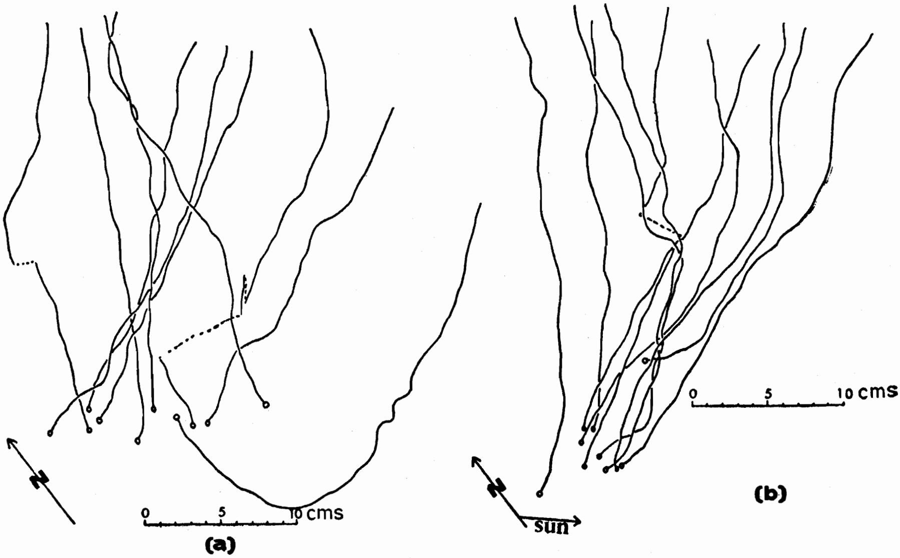

FIG. 2.
(*a*) Tracks of ten beetles from southside swarm released on South bank.
(*b*) Tracks of same beetles on release on North bank.

Orientation of beetles from north bank swarms

The situation was reversed for animals from swarms close to the north side! they tended to head south whether on their own bank or after transport to the other bank. Though inter-individual variation was greater when such beetles were tested on the north bank than was the variability of south-side individuals on their "home" bank, it must be remembered that when the insects were netted and taken from the net for the tests they were for all intents and purposes collected randomly. There is no reason to believe that the difference in results arose from selection of particular individuals. Fig. 3 shows the final headings of 20 individuals released in an open field on the north bank and soon after released again on the south bank. During this time the sun was completely covered by cloud, though the sun's position (127°) was detectable to the eye during the first part of the experiment.

While results of this kind with individuals from swarms on either bank were general, there were exceptional results on occasions. Fig. 4 shows one such. Twenty beetles from a south side swarm were tested on the north bank and headed mainly northwards. Immediately afterwards, however, on the south bank 13 of these beetles headed southwards.

The effect of slope

The observed riverward movements of individuals placed on the ground might have been a movement down the slight slope on top of the bank. Therefore individuals were tested in the open away from the river with the board

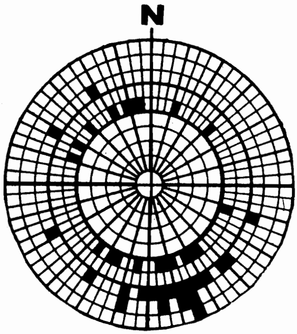

Fig. 3.
Directions taken up by 20 beetles from a north side swarm released in the open on North bank (inner circle) and on South bank (outer circle). 10/10ths cloud.

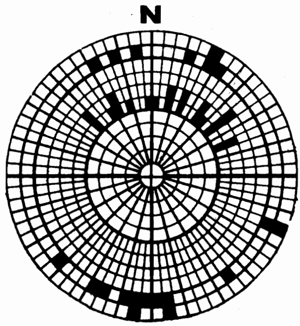

Fig. 4.
Directions taken up by 20 beetles from a south side swarm. Inner circle: released on north bank; outer circle: 12 of same beetles released on south bank.

held at various degrees and direction of slope. Results obtained (e.g. Fig. 5) indicated that slope has little or no effect on the direction of heading by a beetle. This might equally have been concluded from the way in which beetles travelling on the ground maintained their direction despite the fact that they had to surmount obstacles in their path; the changes in the inclination of their bodies had no effect on their orientation. Nevertheless, in the field experiments the board was always carefully levelled with a spirit level.

The effect of landmarks

There is no reason to suppose that the station-keeping behaviour of these swarms when swimming is different from that of the American species (Brown and Hatch, 1929); no doubt landmarks are essential for this purpose. Since the swarms in this part of the Stour were in places where there are trees, a similar use of landmarks in land orientation is clearly a possibility. A cylinder of thin card-

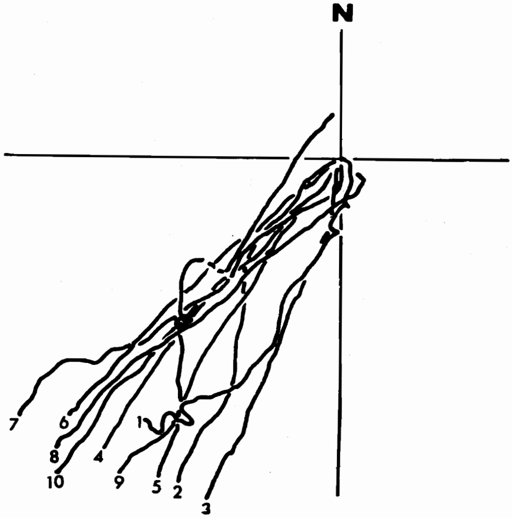

FIG. 5.
Consecutive runs of one individual with different degrees and direction of slope. 1 and 2, 7° slope, North end of board higher; 3 and 4, 13° slope, North high; 5 and 6, level; 7 and 8, 7° slope, South high; 9 and 10, 12° slope, South high.

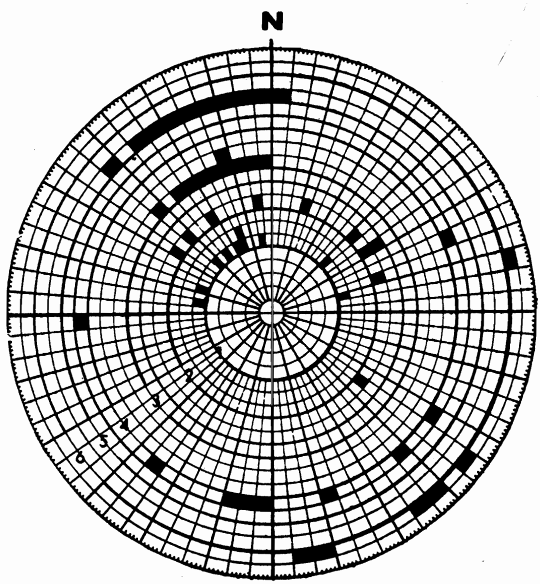

FIG. 6.
Effect of screening beetles, final headings of individuals shown. Eleven-inch screen: circle 1, under tree, sky hidden, circle 2, in open. Twenty-two inch screen: circle 3, in open, top open; circle 4, in open, sheet of paper over top; circle 5, under tree, top open; circle 6, under tree, sheet of paper over top (in this experiment, four beetles did not move from centre of board).

board of height 11 inches was used as a screen. Placed around the compass rose it did not alter the beetles' headings. Similarly, a cylinder 22 inches high had no effect (Fig. 6).

In all these experiments the beetles could view the sky uninterruptedly or through the branches of a tree. But if the top of the taller cylinder was closed with a sheet of paper, headings were altered and some beetles failed to move from the centre. Recording the tracks of beetles with the top of the cylinder closed was clearly very difficult; however, the importance of a sight of the sky was confirmed by an experiment in which the beetles were tested on the bank with a view of the sky, and then re-tested under a tree whose leaves prevented them from seeing the sky above them. Their paths were then more erratic and a predominantly northward orientation was replaced by a random one. If the cylinder was tipped so that light came in under the bottom to one side, the beetles headed in the direction of this higher light intensity.

Effect of proximity to the bank

The northward orientation of south side individuals was not always maintained if they were moved away from the river side (Fig. 7). Beetles tested near the edge were re-tested successively at various distances from the edge. It is plain that as the distance increased the beetles more often moved sunwards.

Constancy of orientation of individuals

Should the riverward orientation be dependent upon sun-navigation, one would expect the angular deviation of the beetles' tracks from the direction of the sun to alter during the day. Such a regular change seems characteristic of sun-navigating insects which maintain a constant direction (e.g. Birukow, 1957). Therefore the headings of a number of individuals were noted when released in the morning, and early and late in the afternoon. Similar massed releases were also made.

When the records of individuals are considered it is seen that they are by no means consistent in their changes of orientation. As Fig. 8 shows, some individuals changed their direction as the sun moved; others oscillated from south-west to south-east and back to west again; and a few maintained their headings throughout the day.

The distribution of headings of ten beetles (each making five runs) at three times during the day are shown in Fig. 8. While the morning directions are not necessarily sunwards, three and a half hours later a greater proportion are directed towards the sun, a tendency which is not maintained three hours afterwards. In other words, though the headings tend to follow the sun's movement, they are not directed at the sun at all times of the day.

DISCUSSION

There appears to be evidence of a riverward orientation of *Gyrinus* individuals when removed from the water surface and placed on land. For individuals from a swarm on the south side of the river this entails a roughly northward heading when put on the south bank, a directional heading that is maintained if the beetles are placed on the north bank. If, for some reason, the beetles find them-

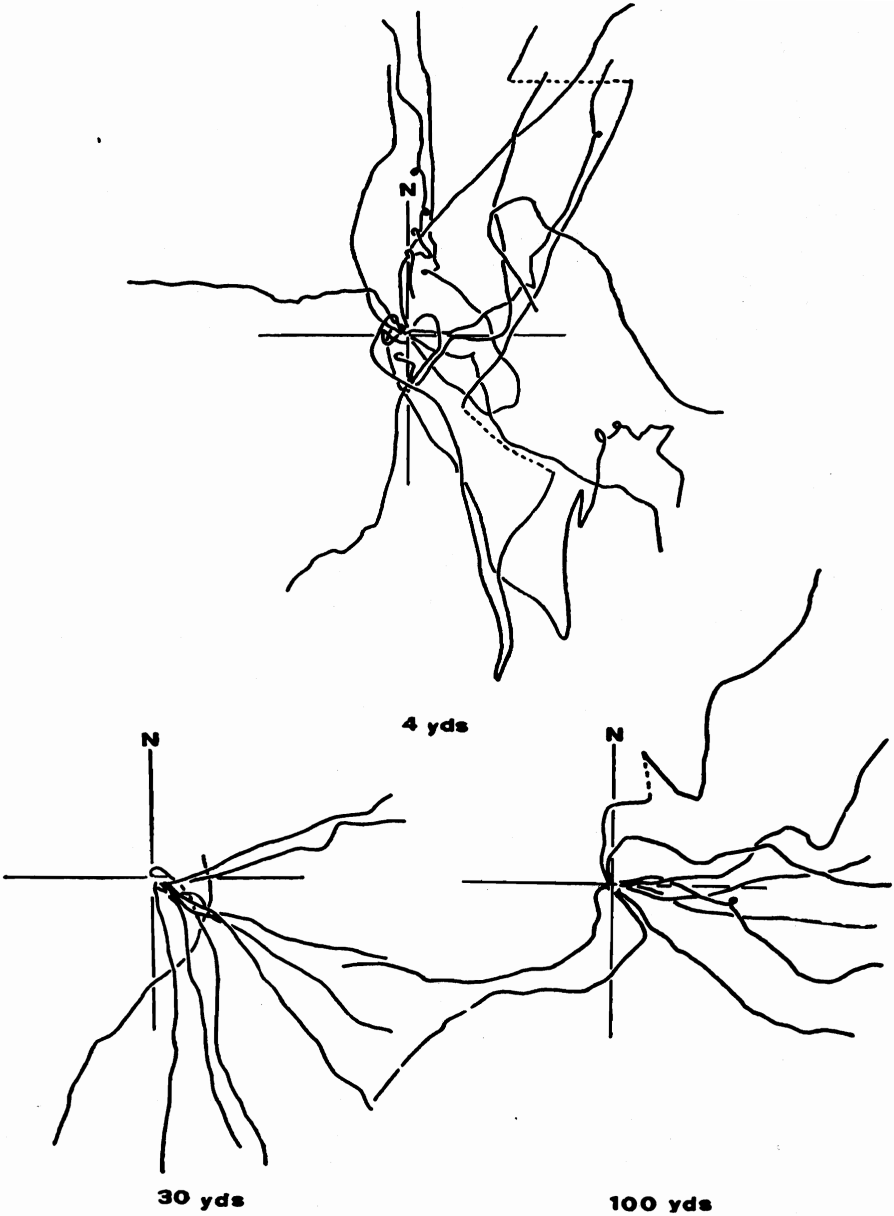

FIG. 7.

Tracks of beetles at various distances from the river's edge. 12 individuals were tested on river edge and found to head predominantly N.N.E. The same individuals were then tested at various distances from the bank (in an open field away from willows lining the bank). 2 beetles were lost after their runs at 4 yards from the river edge. Dashed lines indicate sideways jumps by beetles.

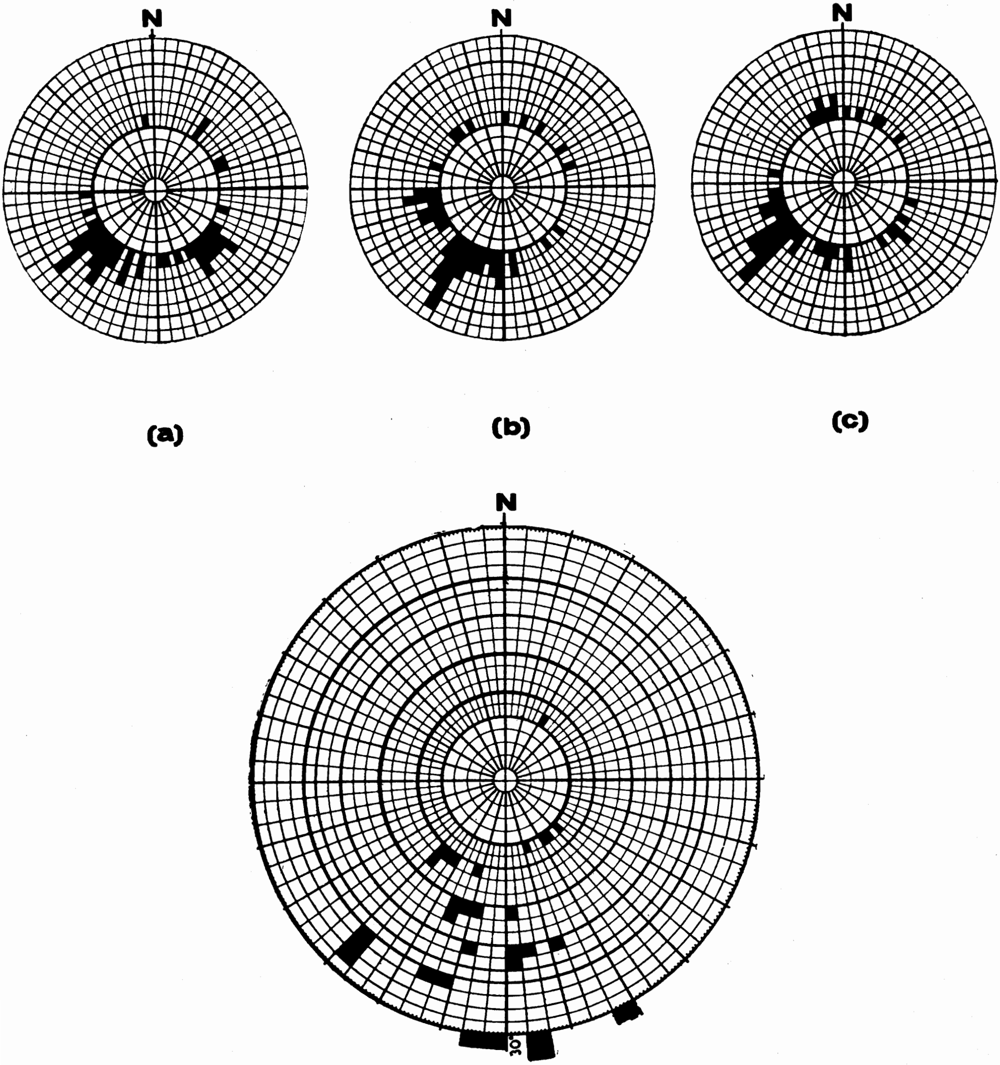

FIG. 8.

Above: Directions taken up by beetles at different times of the day (29 July 1961) (*a*) 10.40–11.15 a.m. (British Summer Time) (*b*) 2–2.30 p.m. (B.S.T.) (*c*) 5–5.30 p.m. (B.S.T.). 10 individuals given five runs each on each occasion. Sun not plainly visible except for a very short period during (*b*).

Below: Tracks of one individual (5 runs on each occasion) over a period of 2 days. From the centre, 1, 10.40 a.m. 29 July 1961; 2, 2.5 p.m.; 3, 5 p.m.; 4, 10.20 a.m. 30 July 1961; 5, 2.15 p.m.; 6, 5.10 p.m.

selves on the bank nearest their swarm they will therefore head back towards the river. The likelihood of their being stranded on the opposite bank is small, under normal conditions, and the failure of the orientation mechanism to return them to the river in this case is not surprising.

It is possible that the biologically adaptive function of this behaviour may be part of the station-keeping behaviour of the swarms. As Brown and Hatch (1929) described for *Dineutes discolor*, *Gyrinus marinus* swarms show two distinct swimming behaviours. In one, all the beetles head upstream making parallel courses and maintaining their position by, no doubt, visual means using the landmarks on the bank in a way similar to that used by *Dineutes*. The other pattern of behaviour is the one which gives the beetles their popular name; the members of the swarms dart about in amongst each other, continually circling and looping, making turns back into the swarm on reaching its edge. Despite the apparently erratic behaviour of its members the swarm nevertheless stays in one place, again, one supposes, by visual orientation to landmarks on the bank. But such a visual system of maintaining position must be impossible on very dark nights. Swarms have been seen to be occupying the same position on moonlit nights, and on nights which though dark were not so dark that silhouettes of trees could not be seen against the sky (personal observation). Under these conditions it seems likely that the beetles could still be using landmarks. However, when these are not visible, possibly the swarm members may crawl out onto the bank to avoid being swept downstream. Then orientation behaviour which led the beetles back to the river by a fairly direct route at first light would be advantageous. This could be the role of the behaviour which has been observed. Such a result would not require a highly accurate heading, anywhere within an arc of 45° to 60° centred upon the most direct line to the river would be sufficient.

In his work on the sun-orientation of *Velia currens*, a water bug which like *Gyrinus* inhabits the water surface but shows a directional orientation when placed on dry land, Birukow (1957) was able to demonstrate that, in the laboratory, the bug shows a continuously altering angular deviation from a light source such that individuals would head approximately 90° to the right of the light at dawn, directly towards the light at midday and at an increasing angle to the left as the afternoon went by. Such orientation ensured that bugs from the particular population he was studying went southwards at all times. Unfortunately no such analysis was possible with *Gyrinus*, as in the laboratory dark room all beetles showed a strong positive phototaxis heading directly towards the light source. When faced with two light beams (Fig. 9) they showed telotactic behaviour for beetles moved towards one or other of the lights and not in between the two. But the tracks of the beetles were conspicuously close to the edge of the beams, where the light intensity was not so great as in the centre.

The strong positive phototaxis in the laboratory may offer a partial explanation for the changes of heading observed in the field when tests were made further and further from the river's edge. When they were moved the beetles were carried into open fields where the usual objects surrounding them, such as trees, were not present. Though these were not acting as orientation landmarks their absence may have caused the beetles to revert to a positive phototaxis towards the sun in place of their usual bankside headings.

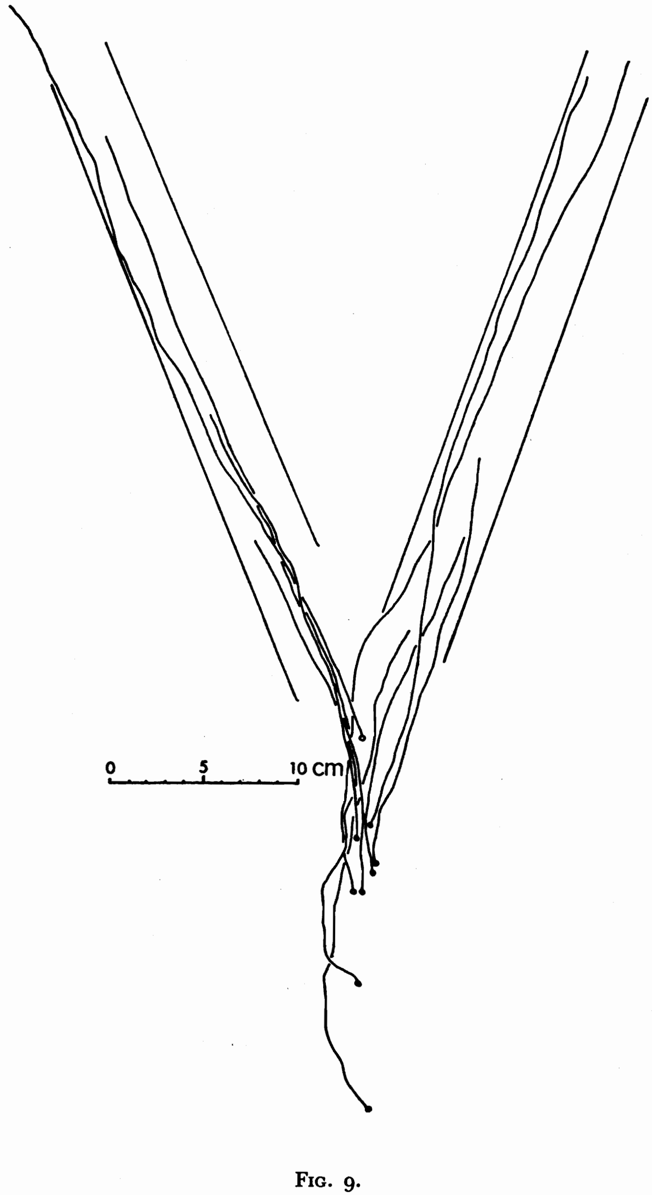

FIG. 9.

Tracks of beetles released in dark room near intersection of two light beams of approximately equal intensity.

Such a supposition raises the possibility that in these experiments one has been dealing with two different behavioural reactions. One, an orientated return to the river, and second, an escape reaction, made in a sunward direction. It is impossible to distinguish between two such behaviours in the present experiments, if indeed such a distinction would be valid.

If members of the southside swarms are to have different headings from those of the north, one supposes that there will be little or no interchange of swarm members between the sides of the river. This would ensure that an animal with the "wrong" responses did not join the swarm. Marking and release experiments carried out with the help of students on this stretch of river suggest that beetles do tend to stay on their own side of the river. Out of fifty beetles caught from a swarm on the south side of the river and released both up and down stream from the swarm's position, only one was recaptured in a north side swarm. The immediate behaviour of beetles on release was to swim upstream near the bank, and most were found the next day to have joined the first swarm they encountered. This is not at variance with the observed return of beetles straight across the river after release on the north side opposite their swarm position (p. 522). This would be a return to familiar station-keeping landmarks. In the displacement experiments beetles were released out of sight of their normal station-keeping landmarks. Like *Velia*

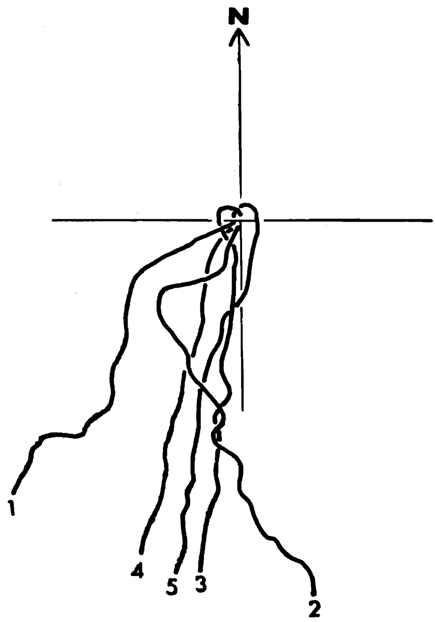

FIG. 10.
Consecutive tracks of one individual moving on differently coloured sheets of paper. Tracks 1–3 on white paper, 4 and 5 on black.

(Birukow, 1957), *Gyrinus* shows different orientation responses whether it is on water or on land.

Clark's (1931) work on *Dineutes assimilis* indicated that the amount of light entering the lower part of this insect's divided eye was of great importance in determining its response to a light beam. It might be objected that in the present experiments the beetles were moving over a white background which would reflect a great deal more light into the lower part of the divided eye of the beetles than is usual. However, the amount of light reflected from the background did not affect the heading taken by the beetle, as the sample tracks in Fig. 10 show. Whether moving on black paper or white, the typical heading for that time was maintained. Similarly if the beetles were allowed to crawl from white onto black and *vice versa* there was no alteration in their responses as they crossed the boundaries. In these conditions the responses of *Gyrinus* are not determined by a balance of stimulation between upper and lower parts of the eye.

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