PHENOMENA OF ORIENTATION EXHIBITED BY EPHEMERIDÆ.[1]

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It is a well-known fact that in alighting Ephemeridæ orient positively to a breeze. I became interested in this reaction and the observations made naturally lead to others on reactions to gravity and to light, and to the results of a conflict between any of these three stimuli.

The observations were made during the summer of 1915 at the Lake Laboratory of Ohio State University at Cedar Point on Lake Erie. Ephemeridæ appear here in almost incredible numbers. When a brood is at its height it is a very common occurrence to find piles of the insects three or four feet square and six to eight inches deep undenelectric lights. At a neighboring amusement resort several carts were required each morning to haul away the dead insects. The species with which the following observations are especially concerned is *Hexagenia variabilis*. The number, variety and arrangement of lights at the resort presented favorably conditions for observing the reactions to light of great numbers of individuals in what may be termed natural surroundings. The equipment used for experiments with air currents and gravity was simple and largely improvised. Nevertheless, since it is not primarily my purpose to measure intensity of stimuli or rapidity of reaction, I believe the results obtained have some interest and value.

Reactions to a Current of Air.

There was a question in my mind as to whether the positive orientation of the Ephemeridæ to a breeze is a response to the breeze per se or whether other factors are concerned. In order to test this I took a piece of glass tubing several inches long and sent through it a weak but steady current of air so directed

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as to strike the insects on the side of the body. They were resting on boards placed horizontally. A few of them flew away but most of them eventually faced the current. Individuals placed on a rough surface, such as a wire screen, which afforded a better foothold frequently tried to walk away. When facing the current of air an individual would raise its long, slender front pair of legs and extend them forward and upward at an angle of about 40 degrees. When held in this way the legs resemble antennae and it is possible they have a sensory function. However, cutting them off had no apparent effect on the reactions here in question. The time required for the turning reaction varied from an almost instantaneous response to two minutes. In the majority of cases the response was gradual and occupied from 30 seconds to one minute. The rapidity of reaction depended upon a correlation between the strength of the breeze and the part of the body it struck.

The influence of the area stimulated is shown in experiments with the wings. The latter are large in proportion to the body and meet over the back in a perpendicular position. They, therefore, present quite a broad surface. When a current of air of an intensity sufficient to blow the wings slightly to one side was directed against them individuals would react in fifteen to thirty seconds, whereas when this current was directed against the thorax or the abdomen the response was slower, if indeed any occurred. A stronger current directed against any of these parts brought about a correspondingly more rapid reaction.

In another series of experiments a current of air was directed from the posterior lengthwise of the body along the dorsal surface of a number of individuals. The response in these circumstances was also an eventual facing about to the current. A current of air striking an individual longitudinally along the mid-dorsal surface is neutral so far as lateral directions are concerned. In the cases here in question the current blew the wings to one side or the other and then as before the insects turned around toward the side on which the strain was exerted.

The experiments were repeated on a group of individuals from which the wings had been removed. The results from a current of air striking the insects on the side of the body were the same as before; the insects faced the current. However, when a current was directed from the rear longitudinally along the dorsal surface of the body the previous results were not repeated. In some cases the insects crawled with the current and away from the point of origin. In other cases they remained stationary and took an attitude similar to that assumed when facing the current. If the current became very strong they either attempted to crawl away or they retained the attitude until blown off their feet. When the current veered sufficiently to strike them on the side they began to turn toward it.

In these experiments with air currents the first noticeable response from the insects was an attempt to hold on to the surface upon which they were resting. This they did by fastening their claws firmly and even changing the position of the legs. When the current became so strong as to make it difficult to remain attached and especially when the body was blown over to one side the insects began to change position, rather hesitatingly it appeared, and to face about toward the direction from which the current came. When an insect reached a position where it did not seem to have difficulty in maintaining its hold it came to rest. This usually meant that it was directly facing the current, although sometimes it stopped at a point between a half and a complete about face. A half about face could generally be made complete by increasing the strength of the current.

When directly facing a current of air an individual is in the optimum position for resistance; it presents the least surface and the claws because of their backward curve have the maximum effect in holding the body. On the other hand when an individual stands sidewise to the current a greater surface is presented, the claws are not in a relatively favorable position and attachment is clearly more difficult. With regard to the more rapid reactions which result when the current strikes the wings it may be said that the proportionately great expanse of the wings above the body's center of gravity gives them such a leverage that the body is more easily tipped over, a strain is more quickly felt and attachment more quickly made difficult. In those cases in which a current struck wingless individuals from the posterior there was practically no obstruction to the current and it consequently did not so easily cause strain or seriously disturb the attachment and there was therefore no turning reaction.

It would appear from the foregoing experiments that the Ephemeridæ do not change position under the stimulus of a breeze until a strain is exerted on the organs of attachment. That this does not merely mean that the response was delayed, until a breeze of a given intensity developed is shown by the fact that a comparatively weak breeze directed against the wings alone had the same effect as was caused by a somewhat stronger breeze against the thorax. There is, therefore, evidence, I believe, for concluding that Ephemeridæ do not orient positively to a breeze because of sensations derived from the breeze per se but that they react positively to tension exerted on the muscles of attachment.

Reactions to Gravity.

The position of Ephemeridæ when resting upon a perpendicular surface is negative with regard to the earth's surface and usually approximately vertical to it, although variations as great as 45 degrees occur. On comparatively smooth surfaces the orientation is more generally an approximation to the vertical, whereas on surfaces such as a wire screen, which affords a good foothold at any angle, variations from the vertical may occur in 50 per cent. of the individuals concerned. Individuals picked up by the wings and replaced head downward, if they are not so disturbed as to fly away, will struggle to gain a foothold. The position of the claws, which are adapted to a vertical position, make attachment rather difficult. This difficulty is increased by the fact that the long abdomen is thrown forward and downward and thus tends to destroy equilibrium. On comparatively smooth surfaces such as a planed board the insects rarely succeeded in maintaining their equilibrium long enough to gain a footing. On a wire screen they were more often successful and once they gained a footing and their equilibrium they retained the new position. The picking up process caused so many of the insects to fly away that other methods were tried. Several individuals were placed in a vertical position on a straw hat held perpendicularly and then the hat was slowly revolved until the insects were upside down. The overhanging abdomen disturbed the equilibrium of some of them sufficiently to cause them to lose their hold and fly off. The others retained their footing, in some cases by changing the position of the legs, and remained in the inverted position for ten to fifteen minutes which was as long as they were watched.

In explanation of the position normally assumed on an upright surface the evidence derived from the experiments seems to indicate that the position taken is not a negative reaction to gravity per se but that it is largely, if not entirely, due to the character of the insect's means of attachment.

Results obtained from experiments performed to test the influence of a breeze upon the position of the insects on a perpendicular surface support this view. A current of air was directed against the side of individuals resting in the normal upright position on a perpendicular surface. As they turned the current was so directed as to bring them still further around. During the process some of them could not retain their foothold and flew off. The others turned completely around and faced directly downward. They maintained the inverted position at least as long as they were under observation, ten to fifteen minutes, which length of time, in view of a constant coming and going among those normally situated, seemed sufficient.

Reaction to Light.

The conclusions with regard to reactions of the Ephemeridæ to light are largely the result of observations made in the amusement resort already mentioned. The observations have to do mostly with artificial light. The insects react negatively to bright sunlight and seek the shade. They are strongly attracted to the lighter colors of artificial light. In the resort there are a great many electric lights of sixteen candle power intensity with colorless glass bulbs. Many of them are attached in a horizontal position to the sides of buildings in such a way that there is a perpendicular surface either above or below them and frequently on all sides.

The reaction to these lights seems to be satisfied if the insects can come to rest within a zone which begins approximately six inches from the light and covers a radius extending outward for about twenty-four to thirty inches. When individuals enter this optimum zone they alight, if a surface is available, and orient themselves in such a way that the body is parallel with a radius projecting from the light. After alighting the insects usually remain at rest, although there may be a certain amount of crawling toward a position nearer the center. This is more often done by those nearer the outer limits of the zone. When the insects are numerous they become arranged in rows consisting of individuals either directly behind one another or slightly to one side and they thus form a striking pattern of radiating lines.

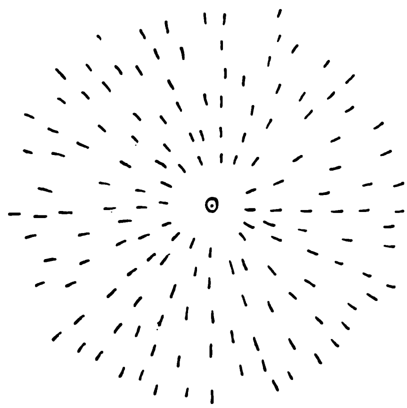

FIG. 1.

The accompanying figures illustrate the positions assumed with regard to lights in different positions and combinations.

The first figure illustrates the position assumed when the surface extends about a light in all directions whether the plane be horizontal or vertical. When any portion of the surface is absent the pattern is of course interrupted to a corresponding extent. The clear zone immediately surrounding the light was approximately six inches wide. I shall call it the excitement zone. Individuals that entered this zone became greatly excited and fluttered about the light in a confused state. There was no evidence to show that individuals at rest deliberately entered the excitement zone. Those immediately bordering on it were rather restless and occasionally in crawling about some were pushed into it and others on taking wing came within the influence of the light.

The second figure shows lights arranged along the lower edge of a perpendicular surface at intervals of twelve to fifteen inches. About each light was the usual excitement zone and upward from this extended the radiating lines of insects in the optimum zone. As shown in the diagram these lines were rarely at an angle of less than 35 degrees. This was due to the fact that below this point the lines from neighboring lights conflicted and caused such confusion among the insects as to obliterate regular alignment. The greatest confusion occurred in the comparatively short space

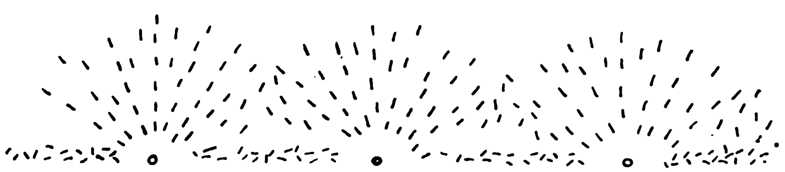

FIG. 2.

between the lights where insects attempting to arrange themselves about one light constantly came into conflict with others attracted to the neighboring light.

When the insects rested on a horizontal plane about a light they faced it. The most striking feature connected with the arrangement of the insects on a perpendicular surface was that the individuals on opposite sides of a horizontal plane passing through the center of a light had opposite ends of the body directed toward the light. The insects below the plane or parallel with it faced the light, whereas those that were above the plane were turned away from the light. In other words all the insects, except those parallel with the horizontal plane, approximated a vertical position with the anterior end uppermost. Those above the plane and with the posterior end directed toward the light were apparently as well content as those below the plane and facing the light.

The position of the insects on a horizontal surface shows that other things being equal they face the light. It is reasonable to conclude that their normal reaction to light is positive. The negative position assumed on a perpendicular surface above a light can be explained, in view of the air current and the inversion experiments, as being due to the difficulty experienced in maintaining a foothold in the inverted position.

Some observations were also made on the relative influence of white and colored lights. On the sides of one of the buildings in the resort there was a succession of alternating white, red and blue lights. The slightly yellowish white bulb attracted the insects in greatest numbers. There was the usual excitement zone and the regular alignment of those at rest. The number of insects about the red and the blue bulbs was decidedly small and as between the two lights about the same. These lights appeared to have a quieting effect on the insects. The alignment was similar to that described for white lights but there was no well-defined excitement zone, in fact the insects crawled about the bulbs without exhibiting markedly abnormal reactions.

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