# Azimuth Orientation of the Dragonfly
## (*Sympetrum*)

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RELATIVELY LITTLE IS KNOWN about the migratory behavior of the dragonflies. Sole summer populations of *Anax junius* in Canada are thought to be maintained by migration from the southern range of their distribution (refs. 1 and 2). Other species, such as *Sympetrum rubicundulum* (ref. 3) in North America, and *Sympetrum striolatum* (ref. 4) and *Aeshna mixta* (ref. 5) in Europe, have been recorded as flying south in early autumn. If these northward and southward movements of the dragonflies are, as they appear to be, unidirectional and well oriented, then it becomes of interest to find out the factor or factors determining the orientation mechanism in migration.

In the past only a few remarks have been made on the orientation of the settling dragonflies. Adults of *Sympetrum sanguineum* are reported to settle in large numbers on telegraph wires or fences. The orientation of these settling individuals is said to be very constant, being related to the direction of incident illumination, so that they face away from the darkest part of their immediate surroundings (ref. 6). This habit of settling en masse on telegraph wires and adopting a constant orientation is also shown by other species of the dragonfly (*Sympetrum costiferum,* Kennedy, ref. 7, *Cratilla calverti,* ref. 8). However, the factor or factors determining orientation are yet to be convincingly demonstrated.

While collecting the dragonfly *Sympetrum* species in the field as an experimental material, we noted a peculiar tendency of the alighting individuals to take a particular direction relative to the Sun. This phenomenon attracted our attention because of possible connection to the migratory behavior as well as to the dorsal light reaction of the species that we have already partly described (ref. 9). Cursory field observation revealed that the direction of orientation is different at different times of the day as it appeared to be somehow related to the displacement of the azimuth of the Sun.

Directional phototactic orientation of many kinds of animals, both in the field and in the laboratory, has been amply described (refs. 10 to 12). There are, however, a small number of observations on the orientation of alighting insects. The contribution of the dorsal light reaction to the equilibrium reaction of the dragonfly *Anax imperator* has been analyzed in detail by Mittelstaedt (ref. 13), mainly in free flying animals. Some other observations exist, but they place emphasis on the reaction of various insects either around their longitudinal axis (banking response) or transverse axis (pitching response) when the light source is placed around those axes (refs. 14 to 16).

Only one report exists on the azimuth orientation of the dragonfly in the horizontal plane. Thus Jander (ref. 17) demonstrated the response of *Calopteryx splendens*, illuminated from various directions in the horizontal plane; but again the emphasis was on the change of posture, not on the change of direction.

In this paper, evidence is presented of directional orientation of the alighting dragonfly relative to the azimuth of the Sun, and an indication is given of the contribution of the wind direction to this orientation. Some preliminary experiments to seek out a possible operative receptor for this orientation will also be noted.

Observed individuals belong to genus *Sympetrum* (Libellulidae, Odonata), of which more than 95 percent are *Sympetrum frequens* Selys, with a very few being *S. darwinianum* S. and *S. infuscatum* S. However, no particular difference in behavior was noticed among those species.

## *FIELD OBSERVATION*

### *General Behavior*

Field observations were performed in an open field on the university campus, which measures about 30 m in east-west direction and about 100 m in north-south direction, and is surrounded with low bushes and bordered with some trees about 5 m high at the north-east corner, the nearest of which stands about 30 m apart from the field's edge.

To avoid possible interference by reflected sunlight from the nearby substratum, data were collected from the dragonflies alighting exclusively on tops of bamboo sticks projecting about 2 m above the ground. It is of interest that there were no directional deviations of the individuals when the tops were lower than 2 m. However, there were directional deviations when the dragonflies were on flat surfaces of high reflectance, such as a white-painted signpost.

Around the end of September and early October, the daily active phase of the dragonfly appears to start at about 8:00 a.m. and continues almost to sunset, the general level of activity being greatly affected by the atmospheric temperature and the amount of sunshine. During warm, but not too hot, brighter, and less windy weather the number of individuals appearing in the field and alighting is more abundant. On the other hand, with winds of more than 2 to 3 m/sec, there is a reduction in number of individuals that can be observed. Thus the measurements were performed mainly on relatively calm days.

Azimuth bearing of the individuals alighting and the azimuth of the Sun were both measured with the aid of a compass attached to a clinometer for geological survey. Wind velocity and direction were measured with the aid of a thermistor-type anemometer.

Alighting individuals were approached from the rear, and the azimuth readings of their longitudinal body axes were measured through the sight attached to the clinometer. In each run of the measurement, 20 to 35 individuals could be observed alighting on the tops of bamboo sticks that were separated from each other by at least 2 m. The readings were taken as fast as possible, mostly within less than 10 min, and at the same time, the direction of the wind and also the wind speed were recorded together with the azimuth of the Sun and air temperature.

Dragonfly alighting appears to be performed in at least four distinct phases. First the dragonfly will approach the stick from a direction that is usually slightly deviated from the final orientation it will take after settling. Second, after a short hovering over the stick, it will alight. Third, while the wings are still stretched horizontally, it will make a final adjustment of the orientation by stepping around on the tip of the stick. During this phase, the head is still pivotted around. Finally, after a short while, the wings will be slightly drooped with the head held fast until startled by a moving object. It is rather curious to observe that when the dragonfly is startled, the first sign of alerting will appear as a jerking movement of the head and also a slight depression of the wings. If the dragonfly is startled with a stronger stimulus, it will take off but will often return repeatedly to the same spot through the almost identical course and alight again after a short while.

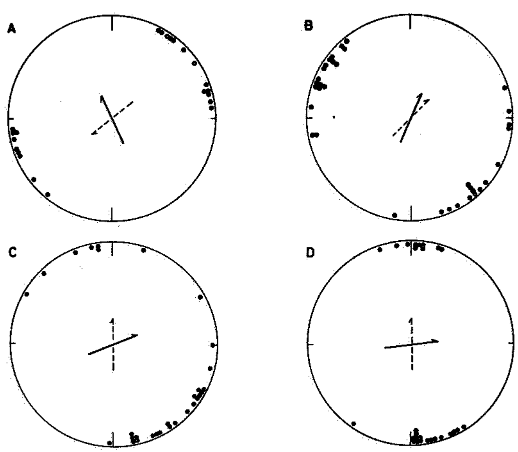


**FIGURE 1. Changes in orientation direction of alighting dragonflies relative to the Sun's azimuth observed on one day. Azimuth is shown in heavy arrows and wind direction in dotted arrows. North is upward. (A) Time of observation: 9:40–9:50 a.m. Overcast: cloudless. Azimuth: SE 25–23° (measured from due south). Wind: NE, 0.2 m/sec max. Air temperature at 2 m above ground: 23° C. (B) 12:08–12:20 p.m. Cloudless. Sun: SW 22–26°. Wind: SW, 0.2–0.6 m/sec. 27° C. (C) 2:30–2:50 p.m. Cloudless. Sun: SW 65–71°. Wind: S, 1 m/sec max. 25° C. (D) 4:18–4:20 p.m. Cloudless. Sun: SW 82–85°. Wind: S, 1.5 m/sec max. 24° C.**

At noon of a hot day (27° C), one individual was found to be taking a very peculiar posture while alighting on the ground: Its abdomen pointed upward almost in the direction of the rays of the Sun (close to 45 deg). In this manner it presented the minimum surface to the direct rays of the Sun, while the wings were drooping to cover the thorax. This kind of posture has been observed in tropical species (refs. 18 and 19).

Also around sunset, on a calm and rather cool day (15° C), many individuals were found to be perched headup on the vertical surfaces of nearby walls to expose their dorsal surfaces to the direction of the Sun. Otherwise, all individuals observed under the direct sunshine in the field have been observed to take a horizontal alighting posture, and their orientation was undoubtedly within a certain azimuth angle.

### *Orientation to the Sun's Azimuth*

Four runs of the observation were performed in one day within their active phase to see the orientation change relative to the movement of the Sun. The measurements were performed on October 1, 1966, a quite calm and warm day. The air temperature around the measured dragonflies stayed 23 to 27° C; there was no overcast nor haze during the daytime. The first measurement (fig. 1A) was performed at 9:40 to 9:50 a.m., with the Sun's azimuth reading at 25 to 23°SE. The measurements were done on 22 individuals, all of which alighted on the tips of the bamboo sticks. The wind velocity was around 0.2

m/sec and from the northeast. Two groupings of dragonflies, both facing almost at right angles to the azimuth of the Sun were clearly recognized. In reference to the wind direction, 13 insects were facing windward, and the remaining 9 faced leeward. About 1½ hr later (from 12:08 to 12:20) 33 more insects were observed. They were also found to be distributed on both sides of the azimuth of the Sun (fig. 1B), the Sun having moved to 22 to 26°SW at this time of measurement and the wind blowing from SW at 0.2 to 0.6 m/sec. Although the wind direction was close to being parallel to the direction of the Sun, the windward individuals numbered 18 and the leeward ones 15. The distribution of the orientation appeared to be somehow more scattered than the previous observation in the morning hour. A possible explanation is the elevation of the Sun from the horizon which, at this time of day, was close to the maximum (45 deg). Two hours later 30 individuals were seen resting on the stick facing again in either direction. The windward portion of the oriented individuals was larger (24 to 6) with the wind blowing from the south at a velocity of 1 m/sec (fig. 1C). The final measurement of the series was done from 4:18 to 4:20, close to sunset. The clustering of the orientation angles of the individuals was at this time more significant than during the other two midday observations, and it was comparable to the results of first observation in the morning. Among the 27 insects, 17 were facing windward and remaining 10 leeward. It is now apparent that the orientations of alighting dragonflies is at least *primarily* related to the azimuth of the Sun throughout their active phase.

The same procedures were repeated on other days, and the results are represented in figure 2. The orientation phenomenon is seen to be the same as that described above. Figure 2A represents an observation performed on a hazy day (80 percent of overcast with thin uniform cloud and with the sun covered). There appeared to be more scatter of the orientation in this kind of weather. One difficulty in attempting to repeat the above observations on hazy days is that, when the overcast is even a little heavier, the number of dragonflies which settle is heavily reduced; therefore, one may not obtain a reliable number of observable individuals.

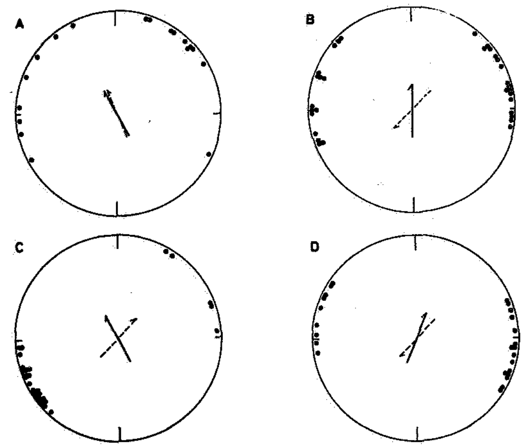


**FIGURE 2. Direction of orientation of alighting dragonflies on separate days. (A) 9:20 a.m. Cloudy (80% overcast). Sun: SE 28°. Wind: SSE, 2 m/sec max. 16° C. (B) 11:30 a.m. Hazy but sunshine. Sun: S 0°. Wind: NE, 1 m/sec max. 18° C. (C) 9:35 a.m. Cloudless. Sun: SE 30°. Wind: SW, 0.5 m/sec max. 22° C. (D) 12:00. Cloudless. Sun: SW 20°. Wind: NE, 0.3–0.6 m/sec. 24° C.**

Since there is an apparent correlation of the azimuth of the Sun to the orientation of dragonfly, all the data are pooled and aligned with regard to the azimuth of the Sun (fig. 3). A notable characteristic of the orientation appears to be that the angle of the orientation relative to the Sun on both sides is slightly greater than a right angle. As seen in figure 4, a statistical analysis shows that the mean value of the angle of orientation with respect to the azimuth of the Sun is 98 deg

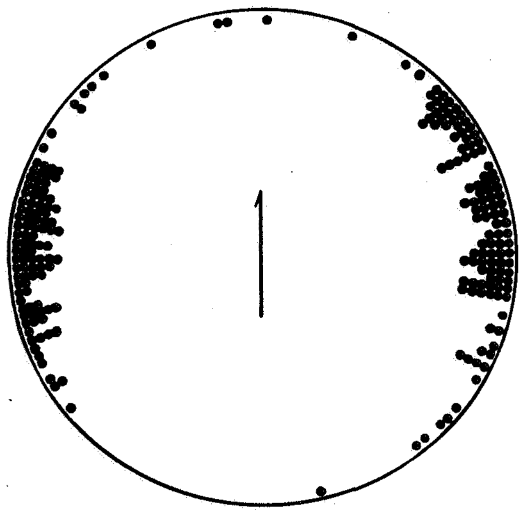

**FIGURE 3. Dependence of orientation on the Sun's azimuth. All data are summarized by superimposing them relative to the azimuth. Arrow indicates azimuth.**

on either side of the direction of the Sun's rays. A correlation coefficient of the oriented individuals facing the right-hand side of the Sun (that is, with one's back toward the Sun) is found to be 0.96, while facing the left-hand side the correlation coefficient is 0.94.

### *Effect of Wind Direction on Distribution*

Although the orientation appears to be primarily determined by the azimuth of the Sun, the wind direction also seems to have some influence on the number of individuals in either half of the Sun's rays. Excluding the one observation in which the wind direction matched the azimuth, the number of individuals oriented in the windward half is without exception more than in leeward half. In total, the ratio was such that there were 2.6 times more individuals facing to the windward half. However, it should be clearly understood that the direction of the wind is not directly related to the dragonflies' orientations (fig. 5). The correlation coefficient between the wind direction and the direction of orientation of the animal is 0.23. This is low enough to exclude the direct connection be-

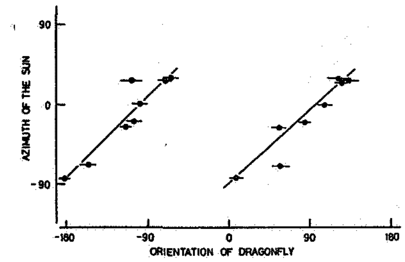


**FIGURE 4. Dependence of distribution on wind direction. Data are shown relative to wind direction. Arrow designates direction.**

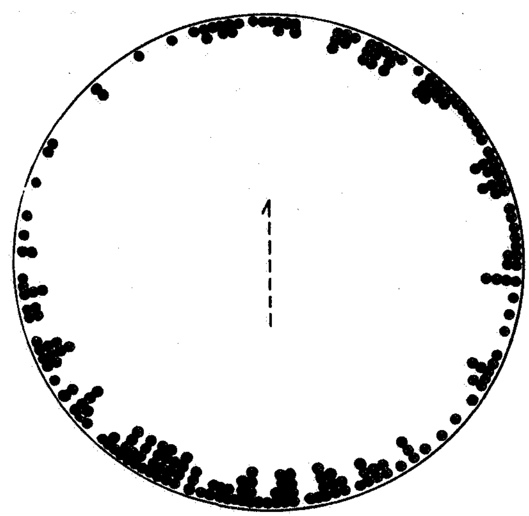

**FIGURE 5. Orientation of dragonflies relative to the Sun's azimuth. Mean value of orientation directions for a number of observations is plotted with standard error against the azimuth. 0 indicates south in both ordinates and abscissae; positive number means easterly side and negative westerly. Regression lines are drawn by the least square method.**

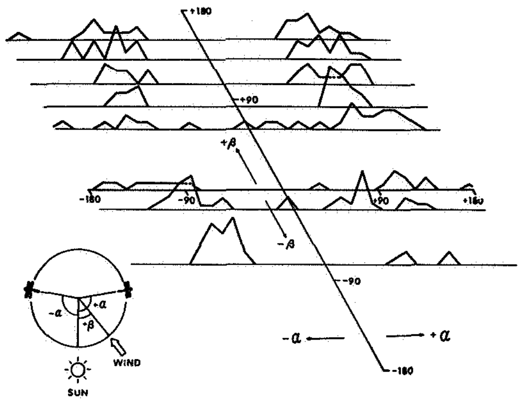


**FIGURE 6. Directional dependence on the Sun's azimuth ($\alpha$) and distributional dependence on wind direction ($\beta$). $\beta = \pm 90$ indicates that observation was made when the wind was blowing at right angles to the Sun, causing dragonflies to face almost upwind or downwind to orient to the Sun. Windward sides (right upper quarter and left lower quarter) contain more insects. Number of insects in each point is normalized.**

tween these two factors, particularly if one considers that the wind tends to prevail in one direction (SE in this locality at this time of the year). In figures 6 and 7, it is shown that only the distribution of the number of individuals facing either windward or leeward is modified by the wind; there appears to be no direct modulation of the orientation.

The results lead us to conclude that the orientation of the dragonflies, when they are settling on an object that gives them rather unobstructed views of the Sun and sky, will be in a direction close to 98 deg from the azimuth of the Sun. The direction of the wind appears to have no determining influence on the dragonflies' orientation. However, indirectly and secondarily the wind direction affects the number of the individuals in the two halves so that more individuals will face windward than leeward.

*Sun and/or Polarized Sky Light*

Directional phototactic orientation of many kinds of animals is attributed to the specially developed ability of the animals for the perception of the plane of the polarized light (refs. 10 to 12, 20 to 22, 23 to 26). A question arises immediatley whether this orientation is one of this category.

Two kinds of field experiments were performed in this regard. First a sheet of polaroid film of 20 by 30 cm was carefully brought over the alighting individuals and placed to occlude the sky. Then the sheet was rotated in either direction to cast the different planes of the polarization to the animals. Despite the difficulty in not startling the animals and making them take wing, 30 individuals were tested without inducing any change in orientation. Secondly a mirror was brought to various positions around the animals to cast the rays of the Sun from different directions while they were covered with a shade to obstruct the direct sunlight but leave the sky visible.

Among 30 trials, 22 individuals responded to the converted direction of the Sun and assumed new orientation exactly in the same

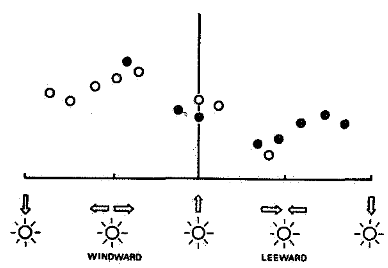


**FIGURE 7. Distribution of insects relative to wind direction. Wind direction measured as an angle from the Sun's azimuth. Number of individuals facing easterly in white circle and westerly in filled ones. Largest number of insects alighted in windward sector (middle portion of left half).**

manner as with the natural Sun (fig. 8A). There appeared to be two prerequisite factors to induce the reorientation: (1) the converted Sun should shine on the frontal part of the animal's head, since the light cast from the side or more caudal to it could not induce the reorientation; and (2) the animal should have just alighted or, if resting with the wings horizontal or slightly drooped, should be just barely startled.

Although much detailed study should be executed, the direction of the Sun appears to be primarily determining the orientation. However, we could not exclude at present the possibility that the polarization plane perception may play a role.

### *Experiment with Rotating Stick*

A stick was raised vertically so that it could be rotated slowly around its long axis and placed in the middle of the bamboo sticks on which the observations were performed (fig. 8B). When the dragonfly came to rest on top of the stick, the stick was rotated slowly in either direction. The animal remained stationary so that it rotated in the same direction as the stick up to a certain degree; then it suddenly regained its orientation relative to the Sun by stepping around. This same procedure was repeated intermittently while the stick was rotating. We have not yet been able to obtain a definite figure for the minimum deviation which triggers the reorientation in this manner, because of variations due to the slight vibration or wind, both of which also appeared to trigger the reorientation. Sometimes the animals were rotated more than 90 deg from the original orientation so that they faced toward or away from the Sun. These animals oriented in relation to the azimuth of the Sun actively through the shorter of the two possible routes.

### *Ocellar Contribution*

The contribution of the ocelli to the dorsal light response of the dragonfly *Anax imperator* (ref. 13) and the phototactic turning tendency of the locust *Locusta migratoria* and the cricket *Gryllus bimaculatus* (ref. 27) has been reported. Our observations show that the reorientation induced by the conversion of the Sun appears to occur only when the light falls within about 90 deg from the front, which is quite close to the lateral extent of the receptive field of the well developed frontal ocellus as determined by electrophysiological method. Therefore, we have attempted to elucidate the possible contribution of the ocelli, particularly the frontal one. More than 100 dragonflies were collected, and both their frontal and lateral ocelli were either painted black or cauterized. Then they

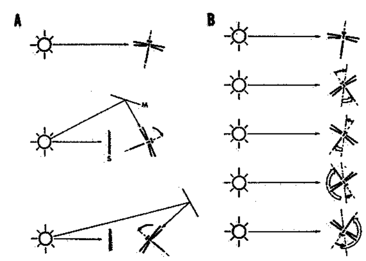


**FIGURE 8. (A) Reorientation of the dragonfly induced by change of Sun's direction with a mirror. Upper: normal orientation. Middle and lower: either clockwise or anticlockwise turn of dragonfly is induced according to altered Sun's direction. Animal will face almost in right angle (98 deg) to new direction of Sun. *M*: mirror. S: shade. (*B*) Reorientation of dragonfly induced by rotation of the stick on which animal is alighting: Uppermost: normal orientation. Second and third: reorientation (black arrow) with small angle rotation of stick (white arrow) in either direction. Fourth and lower: reorientation with rotation of stick in large angle (more than 90 deg). Dragonfly chooses smaller angular movement to take a new orientation, which is also almost at right angles to Sun's direction.**

were put into a cage of 5 by 10 by 3 m with finely meshed net. The cage, standing in the open air close to the experimental field, contained bamboo sticks to provide proper alighting places and the dragonflies were permitted to fly freely in the cage. All the ocellus blinded insects showed quite unpredicatable behavior. The majority of them perched vertically on the surrounding net after a considerable period of jerky flight. In addition, the compound eyes of only one side were blinded in a number of insects before they were released in the cage. Since no individual was seen to behave normally in these cases, it is impossible to say at present whether the ocellus contributes to the orientation. More disturbing is the fact that it was difficult to induce the normal individuals to rest on the tips of the bamboo sticks as long as they were caged, although the mesh of the surrounding net, at least to the experimenter, does not appear to be an obstruction and the cage communicated freely to the outside through the net.

## *LABORATORY EXPERIMENTS*

A number of basic questions still remain unsolved: (1) What is the essential attribute of the stimulus to determine the orientation, i.e., polarized light and/or the Sun itself, although the field observation points toward the latter?

(2) Which sensory organ or organs are mediating this orientation?

(3) To what extent is the orientation related to the dorsal light reaction already reported?

(4) Is this a new type of transverse orientation?

To answer these questions, it should be quite helpful (or, in fact, sometimes compulsory) to have the dragonflies behave in the laboratory as they do in the field. Unfortunately all attempts to date to induce their orientation in the laboratory have proved to be futile. However, in some of the attempts, a number of interesting properties are revealed and will be noted here.

Freshly collected dragonflies were brought into a net cage in the laboratory. The top of the cage was either covered with a transparent or translucent plastic ceiling. A number of sticks were also provided to simulate the alighting positions. Various conditions of illumination were tried without avail. Spectral content of light source, amount of polarization, illumination intensity, and the direction of the illumination were considered. Also the speed of the air current was varied to simulate the wind. Under all these conditions or their combinations, the animals were seen either to take a night perch posture on the side of the stick or on the wall of the cage, with the tail down vertically, or to fly incessantly in a positive phototactic direction toward the light source. Quite interesting was the fact that when the animals were freed in the laboratory where the whole series of artificial light sources were lighted simultaneously, animals were seen to dash toward a small glass window with a closed pane facing the northern sky which was far less bright than was the light from the lamps. Although a few insects were attracted first to the artificial lights, they actually oriented almost immediately to the sky light.

Some animals were tethered, provided with a rotating disc under their legs to measure their turning tendency, and illuminated from the side. The observed responses were clearly of the dorsal light reaction and not of the orientation described in this paper. Of interest again is the fact that the insects under resting conditions did not respond even to the unilateral illumination of quite high intensity. However, a small vibration of the substratum or a weak air puff brought the animal to an alerted condition. When this was done simultaneously with the side illumination, the insect turned the upper part of its head toward the light source and at the same time showed a torque which was developed by the leg movement to face the light source. Wings were removed from some insects which were then freed on the table and various illuminations were applied. No comparable part of the orientation observed in the field was brought out in these cases except the sign of the dorsal light reaction.

It is worthy to note that the dragonfly operates with discrete levels of activity, and the responsiveness of the individual is solely dependent on which level of activity the animal is in. The levels are tentatively divided into four: (1) complete resting level while alighted, particularly during night perching; (2) semi-alerted level, with visual system activated, and oculomotor activity; (3) flight perparatory level, with more sensory systems involved; (4) flight level, with sensory systems in full operation and flight muscles in action.

## *SPECULATIONS AND DISCUSSION*

### *Light Compass Reaction*

The observed orientation agrees with the ordinary light compass reaction in three major ways:

(1) The reflected sunlight from the mirror can induce a change in the direction of orientation so that the reflection of the Sun comes to occupy the direction previously occupied by the Sun itself. This is the classical experment which Santschi (ref. 28) performed on the ant where he found that the Sun directed the ant along its track.

(2) The dragonfly orients in a fixed angle to the direction of the Sun, in a manner of transverse orientation (ref. 29).

(3) The insect turns into new orientation with as little turning as possible and thus chooses the shorter route to reach one of two possible directions. This agrees well with the responses of a number of insects in their light light compass reactions which are described by v. Buddenbrock (ref. 30).

In two aspects, however, the orientation described here does not exactly fit the normal definition of the light compass reaction. Namely (1) the animal is not in locomotion to show the directional orientation although there are some indications that the flying dragonfly also orients relative to the Sun, suggesting that the same orientation mechanism is operative in the insect on wing; and (2) the orientation angle with the Sun is not variable as in the ordinary light compass reaction; i.e., the angle appears to be predetermined innately.

These two different characteristics may indicate that the orientation described here may be a different entity than the light compass reaction.

### *Possible Ecological Values of Orientation*

In early autumn enormous numbers of dragonflies belonging to the *Sympetrum* species can be seen flying in one direction particularly in early morning and late afternoon hours. Casual observation definitely shows the direction of the flight is also at right angles to the azimuth of the Sun and almost unidirectional. Swarming is more common in a gentle breeze and is not observable on windy days. Although these points should be defined more quantitatively to prove their existence more definitely, the orientation during the flight at present seems to be governed by the same factors as in the alighting individuals.

If this is proved to be true, a significant contribution to the understanding of the migratory behavior of the dragonfly will have been made. Assuming the increase in their flight activity after sunrise and close to sunset, and also assuming a prevailing tendency of the wind to blow from only one direction at a certain time of the year at a given locality, northsouth movement or reported appearance of the southern species in north can be readily explained.

Another significance of the orientation may be found in the predatory behavior. Moving small objects against a neutrally lit background is known to induce the predatory response in many kinds of animals. The orientation found here is consistent with this need because the orientation of right angle to the light source gives more chance to perceive the prey in silhouette against the neutrally lit sky.

### *Mediating Receptor or Receptors*

One of the most interesting features of the orientation described here is certainly the orientation angle to the azimuth of the Sun. The angle is about 8° greater than a right angle, and it is fixed at this angle all day. The inference is that there must be a certain structural basis in the mediating receptor that determines this orientation angle. The migrating locust has been described as taking a right angle orientation to the sun (the sun basking response to maintain the warmth of the body by making a maximum exposure to the sunshine, Fraenkel, ref. 31). There is no mention of the particular receptor to mediate this response, which suggests that the temperature change induced by the orientation is an operating factor. In the dragonfly this explanation appears to be inappropriate because of the short latency of response observed in the experiments with the rotating stick and mirror, and the quick settling to the oriented position immediately after alighting. Also a slight deviation of the orientation angle from due right angle cannot be explained at all.

Visual receptors, i.e., the compound eyes, possibly with some contribution from the ocelli should then appear to be the receptors concerned. At present only possibilities can be pointed out without much proof from the experimental data. First it may not be coincidental that the alignment of the ommatidia on dorsal side of compound eye on one side is not parallel to the other side but forms convergent lines of a little less than 20°. If, and only if, the orientation is operated by the perception of the plane of the polarized light by the side of the sky opposite the Sun (which is known to have the strongest polarized light content), the mechanism is such that the animal aligns the ommatidial array parallel to the plane of polarization in the compound eyes opposite to the Sun. The resultant orientation angle can be expected to deviate in just about the same degree from right angle to the Sun as we observed. However, this speculation seemingly contradicts the findings with the rotating polarizer and the mirror conversion of the direction of the Sun. Certainly much more detailed study under controlled laboratory conditions must be done, particularly on the functional analysis of the polarization sensitivity of the dragonfly eyes, before advancing the speculation further.

Second there might exist a clear demarcation of the functional properties of the area of the compound eye in relation to the induction of the turning tendency in the horizontal plane, as is already proved in the dorsal light reflex (ref. 13). Third there still remains a possibility that the frontal ocellus may determine this angle. Electrophysiological analysis of the receptive field of the frontal ocellus reveals that the receptive angle in the horizontal plane is quite wide and appears to extend little more than 90° on both sides of the head. However, the ocellus is so sensitive to the light that photoinhibition of the impulses, first described by Ruck (ref. 32) is found to be induced even after the surface of the ocullus is painted completely black. The light falling of the receptor cells through the thinly pigmented frons was found to be enough to produce the inhibition, thus making the definitive determination of the receptive angle difficult. This also suggests that in order to blind the ocellus, extra care should be taken to prevent the light falling through the surrounding cuticle on the receptor cells.

### *Effect of Wind*

There appears to be a simple explanation for the fact that the wind direction results in an uneven distribution of dragonflies. This is probably produced by the difference in stability of hovering over the alighting position. The insect approaching downwind was more likely to miss the landing point than the one flying upwind. The insect approaching the stick usually makes a short maneuvering course correction immediately before landing to align himself with the wind direction. After alighting, the dragonfly will move to take the orientation to the azimuth of the Sun going always through the shorter of two possible routes. The resulting orientation will thus be at almost 98° to the Sun and likely to face windward.

Finally there is no indication of the "clock" concerning this orientation. The orientation angle is fixed throughout the day and not altered or modified according to the time of the day.

Also it is quite disturbing in the laboratory to not know how to induce the dragonfly to behave and orient as it does in the open field. Without this knowledge the experimental analysis, particularly of the operating stimulus and its receptor, appears to be remote. It is hoped that this knowledge will be discovered and we will be able to make the dragonfly obey the command of our artificial sunlight. Until then the true nature of this orientation remains a riddle.

## *DISCUSSION*

WILLIAMS: Have you tried to analyze the effects of temperature, because the orientation that you described will give it maximum heat?

HISADA: Yes, since the temperature factor is known to be effective in the orientation of the locust. I don't think, however, that this is the case in the dragonfly, because (1) partial illumination of even the head only will induce the reorientation and (2) the latency of the response appeared to be too short to be explained by the temperature effect. It may, however, be possible that the biological significance of this orientation lies in the regulation of the body temperature. On a very hot day, I have observed one individual taking a very peculiar posture in which the animal's tail was held upright directly pointing to the sun, thus exposing minimum area of his body to the direct sunlight. This obelisk-like posture may also be pertinent to the temperature regulation.

WILLIAMS: I have noticed that when dragonflies fly close by, you can detect some that are maimed and thus identifiable individuals. It appears after only a few weeks' observation that there is a territoriality in hunting areas during the evening period. Have you noticed this?

HISADA: Territorial behavior is not apparent in this species, although many other dragonflies are known to have territorial behavior.

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