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Response of the Larvae and Pupae of Aedes aegypti Anopheles stephensi and Culex pipiens to a Moving Shadow-I

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Response of the Larvae and Pupae of Aedes aegypti Anopheles stepehensi and Culex pipiens to a Moving Shadow-I*

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ABSTRACT

This work investigates the behavioural responses of larvae and pupae of three species, Aedes aegypti (L.), Anopheles stephensi Liston and Culex pipiens L. to visual stimuli. The qualitative and quantitative estimates of the response of the larvae and pupae of the three species to visual stimuli of a moving shadow and a moving object without shadow, and the changes of the response with the age of animals (ontogeny) to above stimuli are studied. In all the species a similar rapid diving down response was observed to a moving shadow. The response to the same stimulus is rather affected by the age of the animals which is higher when young but less when old.

INTRODUCTION

The visual stimuli given to the animals is perceived by the visual organs which are compound eyes in most adult insects and in some holometabol insect larvae and ocelli in many insect larvae.

In many insects the compound eyes are exteremely prominent organs. They are composed of a large number of units called ommatidia. These conspicous organs have attracted much attention and their function and structure have been a subject for intensive studies in the various orders of insects.

The insect compound eyes provide poor image formation but are excellent for detecting movements. Many studies on insect behaviour have demonstrated the effectiveness of movement de-

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tection. For example, the behaviour of many insect predators involves a response to a moving stimulus; a dragon-fly nymph captures a moving object (BALDUS, 1) and the wasp, *Philanthus trigranulatum*, directs its predatory attacks to moving objects (TİNBERGEN, 14). Furthermoıe, honey bees, *Apis mellifera*, are more attracted to moving flowers than to stationary ones (WOLF AND WOLF-ZERRAHN, 16) and female mosquitoes are more attracted to moving objects than to stationary ones (SİPPELL AND BROWN, 12). KENNEDY (9) studying optomotor responses of *Ae. aegypti* found that the females are also attracted to dark moving objects.

The movements of objects with shadow cause fleeing in the larvae and pupae of mosquitoes. Their escape responses were usually released by moving an object above them or by decreasing the light intensity. HOLMES (7) studying the larvae of *Cu. pipiens* and *Cu. territans* and MİLLER (11) studying the larvae of *Cu. pipines* induced the escape reaction by passing a black object overhead. The size of the black object and the distance between, the object and larvae in these experiments were not recorded, however, the level of the response was found to be affected by the age of the larvae, temperature changes in the environment and the frequency of application of the stimuli. According to HOLMES (7) and THOMAS (13) response to a moving shadow decreased with the age of the larvae but MİLLER (11) claimed that it increased.

HOCKİNG (6) woıked under natural conditions using the larvae and pupae of *Aedes communis*. He evoked a diving down response in both larvae and pupae by moving opaque objects of various diameters parallel to the surface of the water. He concluded that the diving response was evoked under sunny and overcast conditions. He also found that if the object was moved very rapidly there was no response and that the limiting distance above the water at which a response could be obtained with a given object depended upon its width. However, he did not completely successfully seperate the two factors, the shadow and the movement. So that in his experiments it is not certain whether the larvae and pupae were responding to either the shadow or the movement or to both. In view of this the following experiments were undertaken to investigate separately and in combination, the effects of the two stimuli the sudden decrease in light intensity (shadow) and the movement (without shadow), on the nature of the escape responses, and changes in escape response with age of *Aedes aegypti*, *Anopheles stephensi* and *Culex pipiens*.

EXPERIMENT 1: Response of *Aedes aegypti*, *Anopheles stephensi* and *Culex pipiens* to a moving shadow

MATERİALS AND METHODS

The larvae and pupae used, in these experiments were reared in an insectary with 25 °C constant temperature and about 80 % humidity. The insectary was illuminated with 2 florescent lamps on a 12 hours on and 12 hours off cycle; no natural light was allowed into it. The experiments were also made in the same insectary so as not to effect the behaviour of the animals.

The apparatus used in these experiments consisted of a rotating drum, to which a 12 cm diameter disc was attached with a 30 cm long rod and 6 cm diameter dish containing animals in 2.5 cm depth of water (fig. 1). The disc was covered with a black paper to give the highest contrast with off-white colour of the ceiling. A 60 watt lamp was placed 35 cm above the disc (fig. 1). The disc, 50 cm above the dish was moved with the speed of 35 cm /second, so that the disc passed directly over the dish, its shadow fell on the animals. The light intensity reading taken with a Weston-Master V photographic lightmeter was 12 before shadow of the disc over the dish and it was 6 when the sahdow was over the dish. The subtended angle of the disc was approximately 45° which was 25° bigger than the biggest subtended angle of the disc used by HOCKING (6) in his field experiments on *Ae. communis* larvae and pupae.

The disc was passed over the dish whenever the two following conditions were fulfilled, (i) at least five minute interval had elapsed since the last stimulus presentation and (ii) when at least a standart number of animals were at the surface. Each test group contained 6 animals and the number of animals usually found at the surface aftei 5 minutes was the whole number (6) of the larvae and pupac of *An. stephensi* and *Cu. pipiens* and of the pupac of *Ae. aegypti* and half the number (3) of the larva of *Ae. aegypti.* These were, therefore, taken as the standart number. As the larvae of *Ae. aegypti* were very active and did not stay at the surface for long periods of time, it was very difficult to get more than half the number of the larvae at the surface at a time.

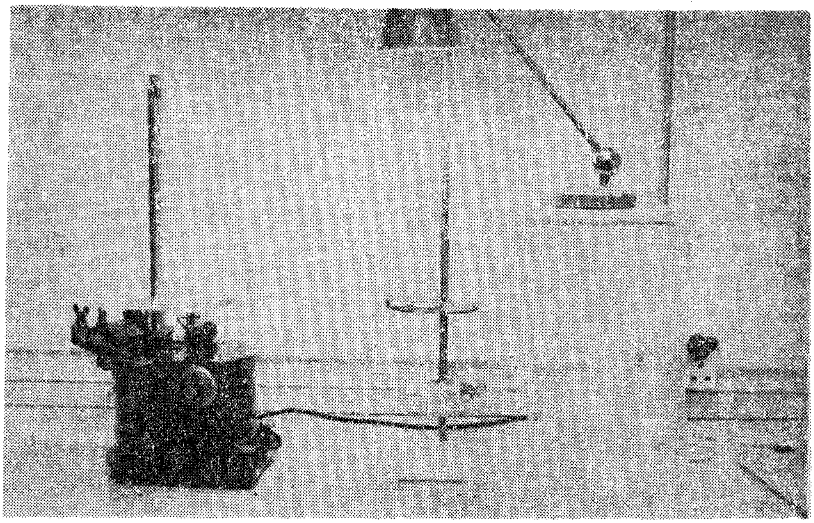

Fig. 1. The apparatus used to conduct the moving shadow experiment. On the left is the kymograph with a 12 cm diameter black disc attached to the rotating spindle of the kymograph and a 60 watt table lamp placed 50 cm above the experimental dish (seen on the right). When the disc was rotated by the kymograph its shadow fell over the experimental dish.

The experiment was repeated with 6 groups of animals and 6 readings were taken from each group for each test. Each group was tested every morning between 9.00 and 12.00 hrs and every afternoon between 14.00 and 17.00 hrs throughout 3rd and 4th instar larvae and pupae in order to determine the change of behaviour with age.

The quantitative results were obtained by counting the number of the animals at the surface diving within 5 seconds of the disc being passed over the dish. According to the counts taken from 6 reading for each group for each test the percentage diving responsc was calculated. The overall mean for each test was calculated from all the groups tested. For statistical comparison each reading was taken into account rather than the percentages.

To determine the quality of the diving behaviour, the animals were observed carefully at the time of application of the stimulus and the style, speed and direction of the swimming were recorded.

RESULTS

(1) *Aedes aegypti*

Behaviour observed.

As the larvae of this species were very active and spent most of their time in moving, it was difficult to obtain an accurate impression of the quality of their response; however larvae responded to a moving stimulus by rapidly escaping downwards from the surface of the water. This escape reaction of the larvae was a rapid swimming movement caused by very rapid bending of the abdomen from side to side. On reaching the floor the larvae stopped for a very short time, then resumed swimming at a much slower rate or feeding on the floor for up to one minute before returning to the surface.

The number of the larvae responding to the stimulus decreased with the age of the larvae (fig. 2).

The pupae of *Aedes aegypti* responded to a moving shadow also by rapidly escaping from the water surface. This escape reaction of the pupae was a rapid swimming movement caused by the flexion and extention of the abdomen moving up and down. After application of the stimulus, the first day pupae spent usually more than 1 minute in rapid swimming between the floor and water surface, before returning to the surface. In natural situation, when the pupae of some species dived down in response to a predator they try to hook themselves to the substrate if possible (Hansell, pers. comm.), by doing so they protect themselves from the predators. In these experiments, no opportunity was given to the pupae to hook themselves to the substrate as the floor of the experimental dish was glass; but this up and down movement of the pupae might be serving the same purpose. In *Ae. aegypti* it was observed that during the time spent in swimming some pupae made intermittent contacts with the surface for only 1 or 2 seconds then continued swimming around before they eventually made a settled contact. The time spent under the water surface in swimming and the number of the pupae responding to this moving shadow stimulus decreased with the age of pupae.

It was observed that the return to the surface could be a passive action in pupae and 3 rd instar larvae but it was always an active swimming in 4 th instar larvae. Passive and active return to the water surface in this species was found by CHRISTOPHERS (2) to be related to the buoyancy of the larvae and pupae; the larvae have a specific gravity equal to that of water in early stages but higher in later stages. Third instar larvae and pupae appear to have a specific gravity less than the specific gravity of water but 4th instar higher.

Qnantitative findings (fig. 2)

The number of the larvae and pupae responding to the moving shadow stimulus decreased within each instar; in the 3rd instar it declined from 99 % on the lst day morning to 92 % on the 2 nd day afternoon before moulting, in the 4th instar larvae from 96 % on the first day morning to 90 % on the 4th day afternoon and in pupae it declined from 77 % on the lst day morning to 4 % on the second day afternoon before emergence.

The response of the pupae dropped suddenly at the beginning of the 2 nd day, from 54 % on the lst day afternoon to 9 % on the 2nd day morning and on the 2nd day afternoon pupae just before emergence the response dropped down to 4 %. The overall mean responsiveness of the pupae was lower than the overall responsiveness of the 3rd and 4th instar significant at $p < 0.01$.

(2) *Anopheles stephensi.*

Behaviour observed.

Before stimulus application, the larvae and pupae of *An. stephensi* were less active than those of *Ae. aegypti* and spent most of their time at the water surface.

When the black disc was allowed to rotate over the larvae and pupae most of the larvae first broke contact with the water surface by active swimming then they either continued swimming or sank down to the floor.

After reaching the floor some of them immediately swam back to the surface but others lay completely still in the same place for up to 2 minutes before returning to the surface with a sudden rapid active swimming .A small proportion of the larvae did not dive down from the surface but responded by sideways running for a short distance without breaking contact with the surface.

Pupae responded to the moving shadow by escaping from the surface. This escape reaction was a rapid swinmmig as in Ae. *aegypti*, produced with flexion and extension of the abdomen. This rapid swimming continued only 1–1.5 cm down from the surface then the pupae floated back to the surface. The return to the surface was therefore always passive with no detectable swimming. All response to the moving shadow ceased towards the end of the lst day pupae.

The return to the water surface was always active in every stage of the larvae but it was always passive in pupae. As the larvae can lie on the floor of the dish their specific gravity must be not less than that of water unlike pupae which float.

Quantitaitve findings (fig. 2)

The response of the 3rd and 4th instar larvae fluctuated from beginning to end of each instar without any obvious decrease or increase in the level of response.

In pupae there was an appreciable response (11 %) only on the lst day morning but this response almost completely ceased as from the lst day afternoon until the emergence.

The overall mean responsiveness of pupae was lower than that of larvae ($p < 0.01$).

(3) *Culex pipiens*

Behaviour observed:

The larvae and pupae of *Cu. pipiens* were less active than those of *Ae. aegypti* but more active than corresponding stages of *An. stephensi*. The larvae of this species responded to the moving shadow by rapidly diving from the water surface. The diving reaction to the floor was rapid movement caused by bendings of the abdomen from side to side as in *Ae. aegypti*. In some larvae this rapid movement continued until the larvae reached the floor but most of them used this movement to break contact with water surface and then sank down to the floor. After reaching the floor they lay there for about 2 minutes or occasionally up to 5 minutes making a few feeding movements and then actively swimming back to the surface.

Application of the same moving shadow stimulus evoked more or less no response in the pupae of this species.

Quantitative findings (fig. 2)

In the 3 rd and 4 th instar there was a general but irregular decline in responsiveness over the age of these two instars.

The pupae of this species showed almost no response to this stimulus.

EXPERIMENT - 2: The response of *Aedes aegypti*, *Anopheles stephensi* and *Culex pipiens* to a moving object without shadow.

MATERIALS AND METHODS

The experiment was conducted to separate the effect of shadow from that of movement and to test the movement alone without shadow. This experiment was set up as in experiment -1, except that the light was placed at about 45° angle to the side of the moving disc keeping the same distance with the experimental dish, to prevent the shadow of the disc falling on the animals, while still having the disc to pass directly over the animals. The number of animals responding was assessed as in the preceding experiment.

Results

(1) *Aedes aegypti*

Behaviour observed and quantitative findings (fig. 2)

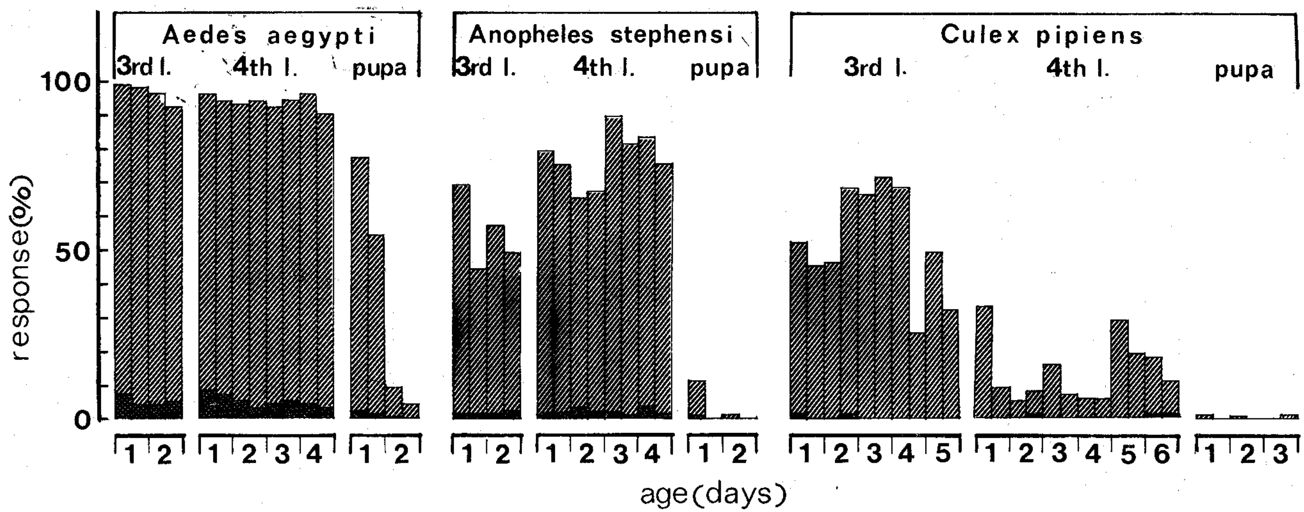

Fig. 2. The mean diving response of 3rd and 4th instar larvae and pupae of the three species to a moving shadow ( ) and to a moving object without shadow ( ) and changes of the response in relation to the ages of animals. The firts column of each day indicates the morning and the second column indicates the afternoon response.

The manner of the escape reaction was the same as in experiment –1, but speed of swimming was much slower than in the experiment –1.

The number of the larvae and pupae responding to this stimulus was significantly lower than the number of the larvae responding in experiment –1 ($p < 0.001$ for each instar).

(2) *Anopheles stephensi*

Behaviour studied and quantitative findings. (fig. 2)

The quality of the response of the larvae of this species given to a moving disc without shadow was apparently the same as the response shown to the moving shadow. But the level of the response to a moving disc without shadow was significantly lower than the response given to a moving shadow ($p < 0.001$ for each instar).

(3) *Culex pipiens*

Behaviour observed and quantitative findings (fig) 2)

Only a few larvae responded to the stimulus of a moving disc without shadow. The level of the response was singificantly lower than the response given to a moving shadow ($p < 0.001$). This experiment was not carried out with the pupae of this species, because the pupae were scarcely responsive even to a moving shadow.

CONCLUSIONS AND DISCUSSION

The behavioural observations on the larvae and pupae of *Aedes aegypti*, *Anopheles stephensi* and *Culex pipiens* showed that a moving shadow is more effective stimuli than the movement in eliciting a behavioural response. The response of the three species to a moving shadow was essentially the same, rapidly diving downwards. However, diving down response of the larvae of *Aedes* and of the pupae of the three species is one of very rapid swimming whereas that of larvae of *Anopheles* and *Culex* is a rapid swimming for a short distance then sinking to the floor. *Aedes* is still active after reaching the floor but *Anopheles* and

Culex are motionless while staying on the floor. The return to the water surface is active in the larvae of the three species but passive in their pupae. However, the return to the surface may not be the part of the overall response to the initial stimulus; oxygen requirements probably cause animals to return to the surface because the speed of swimming up is not as rapid as the descent. In mosquito larvae including the species studied here the same type of escape responses to the same stimuli have been previously described by several authors; HOLMES (7) MİLLER (11) THOMAS (13) and HOCKİNG (6)

In nature a sudden decrease in light intensity caused by a shadow may represent the presence of a predator above, so that the diving response to this kind of stimulus could de anti-predator behaviour since mosquito larvae and pupae apparently have no particular organs of active self-defence.

The difference in the strategy of response of larvae of the three species may offer different type of protection suited to their particular microhabitat. In general, if the prey animals can run faster than the predators, this enables them to get away from their predators. In some cases being inactive may, nevertheless, offer a greater protection than being active; because many predators have rather well developed eye sight so that movement of the prey animals may permit detection ond subsequent capture by the predators. For example, Hansell (pers. comm.) observed that Siamese Fighting Fish (*Betta splendens*) feeding on *Culex* larvae attacked the larvae if they actively swam in water but failed to do so if they sank passively down. The above assumption may equally be true for the predators detecting vibration in the water.

EDMUNDS (3) reviews different kinds of flight behaviour shown by prey insects. He gives examples of insects which continue to escape untill the predator gives up and other which flee first for a short distance then stay motionless for a short time, then move again. The escape reactions of the larvae of *Ae. aegypti* and pupae of the three species fit very well into first strategy and those of the larvae of *An. stephensi* and *Cu. pipiens* to the second strategy, which seems to confirm that the responses shown to a moving shadow are antipredator reactions.

The moving shadow stimulus produces a light intensity decrease and a movement. Separation of the moving shadow stimulus into these two components showed that the animals responded virtually exclusively to the light intensity decrease rather than the movement. These results are contrary to the findings of HOCKİNG (6) in the ıarvae and pupae of *Ae. communis,* since he found that the animals responded exclusively to the movement of the object rather than the light intensity decrease. He came to this conclusion by obtaining the same results under sunny and overcast conditions, without, however, incorporating appropriate controls. The results of the present study do not exclude the detection of movement by the eyes of larvae and pupae as at least a low level of response was observed to the moving object without shadow. Therefore, it appears that besides the light intensity decrease the movement of object is also detected but when the movement alone is presented it does not trigger a high level of response. The higher response to a moving shadow stimulus than to movement alone, which is significant in all three species, could be the result of a simple additive effect; because in essence the moving shadow is a combination of on-off-on light intensity changes and movement stimuli.

As the compound eyes are well developed at least in 4th instar larvae and pupae of the species stuided, it was expected that the movements of objects would be detected especially by *Ae. aegypti,* as its narrower ommatidia have a resolving power higher than that of *An. stephensi*; (KASAP, 9) hovewer, this was not confirmed by the results of this work since none of the species showed a high level of response to a moving object without shadow. It is therefore surprising that the movement is not an effective stimulus for initiating escape responses even in late larvae and pupae which appear to have large, functional compound eyes. It is, however, known as a peculiar fact that an animal does not necessarily react to all changes in the environment which its sense organs perceive, e.g. adult *Dytiscus marginalis,* which has perfectly well developed compound eyes and can be trained to react to visual stimuli, does not react at all to visual stimuli when hunting a prey so that a moving prey stimulus in a glass tube does not release or guide any response (TİNBERGEN, 14). Another example is that in courtship behaviour of grayling butterfly, *Eumenis semele*, the mating pursuit of males is released by a stimulus situation in which colour has no influence although they are capable of discriminating yellow and blue in feeding (TİNBERGEN, 15). From the examples it is seen that although an animal is capable of detecting a stimulus it may respond to it in one stimulus situation but may ignore it in another. This may also be the case in the larvae and pupae of the mosquitoes studied here that animals with well developed compound eyes may be detecting movement or other visual patterns in other contexts, e.g. in feeding but they may not be responding to the movement in predator detection.

Overall responsiveness of the larvae and pupae of all the three species studied changed with age. In the larvae of *An. stephensi* and *Cu. pipiens* it fluctuated during the period of each instar, in *Culex* usually increasing every afternoon in accordance with the increase in the room temperature and decreased in the last day of each instar. This decrease in the last day might be due to the other morphological and physiological changes going on in the pre-ecdysial stage, but since this stage starts at different times in different individuals (HİNTON, 5) it is rather difficult to determine whether the decrease in the responsiveness is closely correlated with the onset of pre-ecdysial stage. However, there was a more or less gradual decrease in response during each larval instar of *Ae. aegypti* to the visual stimuli used. Here again effect of the pre-edcysial stage on the responsiveness is not certain.

The response of the larvae of *Ae. aegypti* is negatively correlated with the age of the animals. These results are hard to explain, however, some conclusions may be drawn. Firstly, in mosquitoes, the larval stages are known as the only growth phase after hatching out (GİLLETT, 4). During this period the animals may concentrate on the growth so that the external stimuli become less and less effective. HUMPHREY (8) also, while discussing the decrement caused by the habituation, pointed out that a response decrement results from maturation, which is different from the habituation in being irreversible.

Secondly, as has already been discussed, the response to the shadow are most likely to be anti-predatory, but animals may also protect themselves from predators by being less active.

Thirdly, the response decrement is consistent with the increase in the oxygen requirement of the animals. The older larvae of *Cu. pipiens fatigans* spend much longer time at the surface than the younger larvae (THOMAS, 13) suggesting that the oxygen needs of older larvae is higher than that of younger larvae. For example it was occasionally observed in *Aedes aegypti* that if the stimulus was applied immediately after arrival of the larvae to the water surface the larvae did not respond at all, so that the oxygen need may here have an inhibitory effect on the responsiveness of the larvae. As the larvae of *Cu. pipiens* spend most of their time at the water surface and descend to the bottom only for feeding, their response should be rather less influenced than the response of the *Ae. aegypti*. The larvae of *An. stephensi* are surface feeders and live attached to the water surface. Therefore during normal resting and feeding they should not suffer any oxygen deficit so that their response may not be depressed by the oxygen requirement.

In the three species the overall responsiveness of the pupae was lower than that of larvae; after pupation the decline in responsiveness with age continued during the whole pupal stage. This stage is known as a transitional stage in which although no more growth occurs, there are drastic changes towards the development of adult characters at the expense of which efficiency of nervous and sensory mechanism of pupae may have to be sacrificed. However, it was observed that if pupae responded they could swim vigorusly; therefore although pupae are capable of swimming vigorously they prefer not to move possibly to allow the development of adult in pupal skin; this preference may also favour their being less recongnisable by the predators as discussed previously for larvae.

Also in pupae there is an air cavity in thorax. With the developing adult in pupal skin the amount of air in thoracic cavity increases and animals become more and more buoyant so that they can not swim for a long time in water; if they stop swimming they float back up to the water surface. The response threshold of pupae is raised because, although vigorous swimming is still possible, its effectiveness is reduced due to buoyancy. However, it was observed in pupae of *Trichoprosopon ulopus*, *Cu. secundus* and *Weyomia pertinana* by Hansell (pers. comm.), pupae when swimming at the bottom try to hook themselves to the substrate to avoid floating. A similar phenomenon was also observed in the species studied here. For species capable of doing this there is more value in attempting response as pupae. It will be interesting to know how widespread this ability is among other mosquito pupae.

Another factor that could account for or contribute to lowering of response in pupae is the anatomical evidence found by CHRİSTOPHERS (2) that the cuticle of pupae is much thicker than that of larvae. The thicker cuticle may allow less light to reach the eyes.

One or any combination of these four factors discussed above could account for pupae being less responsive than larvae.

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ÖZET

Bu çalışma Aedes aegypti, Anopheles stephensi ve Cluex pipiens larva ve puplarının ışıksal bir uyartıya olan davranışlarını kapsamaktadır. Işıksal uyartı olarak hareketli bir diskin gölgesi ile hareketli fakat gölgesi hayvanların üzerine düşmiyen bir disk seçilmiştir. Her iki etkiye gösterilen davranışlar karşılaştırılmış ve ayrıca davranışın yaşla olan ilişkisi araştırılmıştır. Her üç türün hareket eden cismin gölgesine hızlı bir biçimde dibe dalmak suretiyle davranış gösterdikleri ve bu davranışın sayısal olarak yaşla azaldığı saptanmıştır.

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