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Concealment behavior of nymphs of Blaberus giganteus L. (Dictyoptera: Blattaria) in relation to their ecology

by

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In a laboratory culture of the tropical cockroach, *Blaberus giganteus* (L.) we observed that, whereas adult insects almost invariably climbed the wire screen sides of their cage, nymphs always burrowed in the debris of sawdust and feces lying on the floor. We therefore decided to investigate the behavior reactions involved and their physiological bases.

REACTIONS TO LIGHT

Reactions to light were tested in a choice-chamber consisting of an oblong wooden box (35 x 10 cm). The floor of the area consisted of wire screen covering petri dishes that contained moist filter paper to maintain a high humidity within. One half of the choice-chamber was covered with transparent plastic, the other with cardboard covered with aluminum foil to exclude light. The intensity of illumination from fluorescent lamps falling on the lighted side of the area was about 1,500 lux. Five adult and five nymphal *B. giganteus* were placed in the arena and their positions in the light or dark were noted at intervals of 10 min. at room temperature (22.5 $\pm$ 1 C). If an insect was found resting across the midline it was counted as being in light or dark according to the position of its head. The transparent and opaque covers were interchanged after each read-

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ing and the insects mildly stimulated by tapping the bench on which the choice-chamber was resting. In all, ten experiments, each consisting of ten readings were carried out, giving 1,000 position records, 500 for adults and 500 for nymphs. The apparatus was rotated through 180° between experiments to eliminate any possible extraneous influences.

The results, expressed as percentages of the position records were as follows: *in light*, adults 53%, nymphs 31.5%; *in dark*, adults 47%, nymphs 68.5%. Chi-square analyses, each with one degree of freedom, indicate no significant preference for light or darkness on the part of adults ($X^2=2.05$) but a highly significant photonegative response from the nymphs ($X^2=67.70$, $p<0.001$). Although the adults exhibited neither negative phototaxis nor photokineses, they were clearly able to appreciate the difference between light and darkness and would frequently make jerking movements when suddenly exposed to illumination.

The cockroaches used in the experiments described above were tested in daytime and had been raised under a light-dark regime during which they were illuminated between 0600 and 2100 hrs and kept in darkness throughout the night. The effect of the circadian activity rhythm (CLOUDSLEY-THOMPSON, 2) was investigated by repeating the work on insects whose rhythms had been reversed. This was done after subjecting them to reversed lighting so that they were illuminated between 1800 and 0900 hrs and kept in darkness during the day for at least one week previously. The following results were obtained: *in light*, adults 34%, nymphs 32%; *in dark*, adults 66%, nymphs 68%. From these it can be seen that during the nocturnal phase (scotophase) of their circadian rhythm, adult *B. giganteus* are definitely photonegative ($X^2=52.48$, $p<0.001$), while the negative response of nymphs to light ($X^2=66.24$, $p<0.001$) is practically the same in both nocturnal and diurnal phases of their rhythms.

REACTIONS TO SUBSTRATE

In order to investigate the responses of the insects to substrate, a choice-chamber was constructed of similar dimensions to that used for testing reactions to light. The floor on one side of the arena, however, was filled to a depth of 3 cm with debris of sawdust and feces from the culture chamber, while that on the other side consisted of wire screen at the same level. Experiments were carried out as before, the number of adults and nymphs resting on the wire screen and on the debris or buried in it being recorded at intervals of 10 min. Buried insects were dug up at each count, and the others also thoroughly disturbed. The experiments were carried out alternately in light (1,500 lux) and in darkness, in order to determine the influence of light on the responses of the insects.

The results (Table 1) were again analysed by the chi-square method with one degree of freedom, and can be summarized as follows:

1. Adults showed no preference for either the wire screen or the debris ($X^2=2.05$) but nymphs showed a highly significant preference for debris ($X^2=33.80$, $p<0.001$).
2. Nymphs buried themselves much more than did adults ($X^2=143.14$, $p<0.001$).
3. Both adults ($X^2=16.49$, $p<0.001$) and nymphs ($X^2=4.14$, $p<0.05$) buried themselves significantly more often when exposed to light than when in darkness.

TABLE 1

Position records (expressed as percentages) of B. giganteus *on wire screen, and on debris or buried beneath it, both in light and in darkness.*

Wire Screen		Debris		Buried	
Adults	Nymphs	Adults	Nymphs	Adults	Nymphs
		Light			
50	34	34	8	16	58
		Dark			
56	40	39	13	5	47

THE BURYING RESPONSE

The burying reactions of adult and nymphal *B. giganteus* were investigated with the aid of a cylinder composed of five cardboard rings, each 10 cm in diameter and 5 cm in height. When placed one above the other and filled with debris, a column 25 cm in depth was produced. In order to achieve stability, an outer sleeve of cardboard was made to fit around the five rings. Five adult *B. giganteus* and five nymphs were placed on top of the debris and their positions in the various cardboard rings noted after various intervals of time. Counts were made by separating the contents of each ring by means of a sheet of cardboard, and tipping them into a dish so that the insects within could be counted. Tests with a photo-electric meter showed that no light penetrated below 5 cm of debris.

Preliminary experiments showed that some nymphs could bury themselves to a depth of 15 to 20 cm within 30 min and that, when left in the apparatus overnight, no deeper penetration was achieved. Experiments were therefore done over varying durations (30 min - 7 hrs, and overnight) and the results based on 250 position records for nymphs and adults and expressed as percentages, are as follows:

On surface, adults 88%, nymphs 37.5%; *0-5 cm*, adults 11%, nymphs 29.5%; *5-10 cm*, adults 1%, nymphs 18.5%; *10-15 cm*, adults 0%, nymphs 12%; *15-20 cm*, adults, 0%, nymphs 2.5%; *20-25 cm*, adults 0%, nymphs 0%.

From these percentages it can be seen that nymphs not only burrow more readily, but also more deeply than do adults. The possibility that burying by the adults might be hampered or inhibited by the presence of the wings was eliminated by removing both pairs of wings from five adult cockroaches. When tested in the cylinder, however, these showed no tendency whatever to burrow. It also seemed possible that the burrowing propensities of the nymphs might be under hormonal control. Nymphs from which the legs had been removed were therefore joined in parabiosis to the dorsal surfaces of adults by means of a glass capillary tube sealed with paraffin. Even this treatment, however, did not induce the adults to burrow.

THIGMOTACTIC RESPONSES

The flattened shape of these cockroaches, and particularly of the nymphs, strongly suggests an adaptation to living in crevices. Responses to crevices were tested by placing five adults and five nymphs in a cardboard box measuring 25 x 30 cm. Artificial crevices were constructed in the two ends of the box by means of transparent 13 x 25 cm polyethylene sheets projecting from the floor at an angle of 30°. The numbers of adults and nymphs in the crevices —that is, with their backs actually touching the polyethylene—were counted at intervals of 10 min. Experiments were carried out alternately with the insects exposed to light (about 1,500 lux) and in darkness. The box was rotated 180° after every two observations. The results, based on a total of 1,000 position records, are given in Table 2.

When subjected to chi-square analyses as before, the results can be summarized as follows:

1. In darkness, nymphs were found significantly more often in crevices than outside ($X^2=30.98$, $p<0.001$).
2. In light, nymphs were also more often in crevices than not ($X^2=90.00$, $p<0.001$).
3. In darkness, adults showed a significant avoidance of crevices ($X^2=10.02$, $p<0.01$).
4. In light there was no significant difference between the number of times adults were found in crevices or outside ($X^2=0.40$)..
5. A chi-square test for homogeneity showed that the number of times nymphs were found in crevices in light was significantly greater than the number of times they entered crevices in darkness ($X^2=9.94$, $p<0.01$).

TABLE 2

Position records (expressed as percentages) of B. giganteus *within crevices or outside.*

In crevices		Outside crevices	
Adults	Nymphs	Adults	Nymphs
	Light		
48	80	52	20
	Dark		
40	68	60	32

TRANSPIRATION

TRANSPIRATION RATE: The possibility that the greater tendency of nymphs than adults to burrow might be related to differences in transpiration rate under normal physiological conditions was investigated as follows. Eight pairs of adults and nymphs were placed in small cardboard containers and exposed in desiccators for four or five consecutive periods of 24 hrs at 27 C in 10% relative humidity (over a saturated solution of lithium chloride). Their rates of water loss per day were determined by weighing, 30 measurements being taken in each case.

Results were standardised by converting the figures for water loss to sq cm of surface area. After the surface areas of weighed adults and nymphs had been ascertained by cutting up the cuticle and fitting it over squared paper, it was possible to ascertain surface area of individuals from their respective weights by means of the formula $S = k\ W^{2/3}$, where S= surface area, W= weight and k is a constant. For *B. giganteus* a value of $k = 10$ was obtained with both adults and nymphs. This is the same value that MEAD-BRIGGS (6) obtained for *Periplaneta americana.*

The means and standard errors for water loss under the conditions described above were: *adults* 5.36 $\pm$ 0.39 mg/cm²/day; *nymphs* 4.67 $\pm$ 0.37 mg/cm²/day. It is apparent that no significant differences occur between the rates of transpiration from adults and nymphs. These figures compare with 10 mg/cm²/day from *P. americana,* 8.6 mg/cm²/day from *Blatta orientalis,* and 7.3 mg/cm²/day from *Blatella germanica* in dry air at 30 C according to GUNN (4). The comparatively low rate of water loss from *B. giganteus* may be correlated with the warmer environment normally occupied by this species in nature.

"CRITICAL" CUTICULAR TEMPERARATURES: Water loss through transpiration at different temperatures was measured by weighing adults and nymphs before and after exposing them to dry air in a bottle containing activated alumina heated to various temperatures in a water-bath. This classical method (WIGGLESWORTH, 7) has been criticised for several reasons (BEAMENT, 1; EDNEY, 3), but it has the advantage of simplicity and the fact that it enables valid comparisons to be made between different species. In the present work, the object was to compare the "critical" temperatures at which the cuticular lipids of nymphal and adult *B. giganteus* become comparatively porous.

The results of this experiment (Table 3) indicate that the nymphal cuticle is at least as resistant to water loss at low temperatures as is the adult cuticle, and that at high temperatures it is probably more resistant. It is also evident from the data that the "critical" temperature of both types of cuticle is between 50 and 55 C, which is considerably higher than that given for *Periplaneta americana* (betweem 30 and 35 C) in a comparable investigation by MEAD-BRIGGS (6). Certainly cuticular transpiration in *B. giganteus* ought not to be a factor influencing the behavioral differences under consideration.

ODORS AND DEFENCE

One of the ways in which cockroaches escape from predators is by the secretion of offensive fluids which have been described in a number of genera (GUTHRIE & TINDALL, 5). *B. giganteus* is no exception and the adults, but not the nymphs, produce a pungent odor for a few seconds on being disturbed. Pairs of adults and nymphs were concealed in beakers covered with aluminum foil through which holes had been punched, and volunteers asked if they could detect any difference in the smell emanating from the beakers. In every case a strong scent was detected from the beakers containing adults but not from those containing nymphs. Newly moulted adults do not smell and the odor seems not to develop appreciably at least until two days after metamorphosis.

Another way in which adults show greater powers of offence than nymphs lies in the fact that the tibial spines of their legs are larger and harder. When caught in the hand they can administer a sharp prick which the nymphs are quite unable to do.

DISCUSSION

Temperature and humidity preferences in cockroaches are not clearly defined. *B. giganteus* has a preferred temperature range of 20-33 C (GUNN, 4) but this probably depends upon the temperature to which the insects have been conditioned. The responses of cockroaches to different humidities are likewise not clear cut as in some other insect species: such responses appear to vary according to the temperature and the state of hydration of the animals tested (5). We did not, therefore, attempt to compare the responses of adult and nymphal *B. giganteus* to temperature and humidity. The water relations of adults and nymphs are very similar, however, and aktograph experiments have failed to disclose any appreciable difference in their circadian rhythms (CLOUDSLEY-THOMPSON, 2). Indeed, the main adaptive difference between the two stages seems to lie in the ability of adults to produce offensive odors. It is in regard to this character that we believe the burying habits of the nymphs

TABLE 3

Water loss (expressed as mg/cm²/hr) of adult and nymphal B. giganteus *at increasing temperatures in dry air**

Temperatures							
35	40	45	50	55	60	65	70
Adult water loss							
1.7±0.2	1.8±0.3	3.0±0.2	3.9±0.5	9.0±0.5	9.3±0.9	10.3±1.4	14.1±1.4
Nymphal water loss							
1.1±0.3	1.0±0.3	1.9±0.5	2.1±0.5	4.1±0.6	4.3±0.8	4.2±2.0	8.8±1.2

* Means and standard errors given for six adults and six nymphs.

are correlated. Adults are probably protected by their smell and tibial spines, nymphs by burrowing. We have been unable to detect any physiological difference to account for the ecological and behavioral distinctions between reactions of adults and nymphs to light, substrate, and crevices.

SUMMARY

Nymphal *Blaberus giganteus* (L.) tend to bury themselves or hide in crevices whenever possible, whereas adults do not do so to any great extent. Burrowing of both adults and nymphs takes place significantly more in light than in darkness. Nymphs are photonegative at all times; adults only during the nocturnal phase of their circadian rhythm. Adults avoid crevices in dark, but show neither avoidance nor preference for them in light. Nymphs, on the other hand, show a positive reaction to crevices in both ligbt and darkness, but the response is significantly greater in light. Transpiration rates and "critical" cuticular temperatures are essentially the same in both adults and nymphs. The nymphal cuticle is probably more resistant to water loss at higher temperatures than that of adults. We conclude tbat concealment behavior in nymphs is probably correlated with escape from predators rather than with physiological factors because, unlike the adults, the nymphs do not produce offensive odors and their tibial spines are less sharp.

RESUMEN

Las ninfas de *Blaberus giganteus* (L.) tienden a enterrarse o a ocultarse cuando quiera que les sea posible, mientras que los adultos lo hacen muy raramente. El acto de enterrarse de los adultos y de las ninfas ocurre significativamente más en la luz que en la oscuridad. Las ninfas son siempre fotonegativas; los adultos lo son únicamente durante la fase nocturna de su ritmo circadiano. Los adultos evitan las rendijas en la oscuridad, pero no muestran ni preferencia ni aversión a ellas en la luz. Las ninfas, en cambio, muestran una reacción positiva hacia ellas en la luz y en la oscuridad, pero la reacción es significativamente mayor en la claridad.

Las gradientes de transpiración y las temperaturas cuticulares "críticas" son esencialmente las mismas, tanto en los adultos como en las ninfas. La cutícula de las ninfas es probablemente más resistente que la de los adultos en relación con la pérdida de agua a temperaturas más elevadas. Probablemente la acción de ocultarse de las ninfas tiene correlación más bien con el acto de escaparse de los animales de presa que con los factores fisiológicos porque, a diferencia de los adultos, las ninfas no producen olores desagradables ni poseen espinas tibiales tan puntiagudas.

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