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Colonization and Biology of *Opifex fuscus**

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Abstract

Opifex fuscus is a mosquito easily maintained in the laboratory, and its unique mating requirements are readily met. Adults emerge with large energy reserves and are autogenous, so sugar and blood meals are not necessary for the first gonotrophic cycle. Rearing is simple in 75% sea water at ca. 25° C., requiring only common larval foods. Cheesecloth pads partly immersed in water are good oviposition substrates and the eggs can be stored for up to three months easily. The only really unique feature in the rearing process is the need to keep males with pupae to assure copulation at or soon after emergence. Males of this species pursue pupae and mate with the emerging females, often before they are out of the pupal skin.

NEW ZEALAND'S *Opifex fuscus* Hutton is a large, blue mosquito with several unique morphological and behavioral characteristics. It was first described as a crane fly (Hutton, 1902), breeding in brackish rock pools above high tide level. The adult males remain on these pools, pursuing pupae and mating with the females as they emerge from the pupal skins (Kirk, 1923). We wished to compare these male habits with similar behaviour in Florida's crabhole mosquitoes, *Deinocerites cancer* Theobald, hence the observations here reported. Further information on the distribution, morphology, and behaviour of *Opifex* is found in a rather limited literature (Belkin, 1962; Edwards, 1926; Graham, 1929; Marks, 1958; Miller, 1922; and Miller and Phillips, 1952).

MATERIALS AND FACILITIES

The collections of *Opifex* in New Zealand were obtained through Professor L. R. Richardson, of Wellington University, to whom we are greatly indebted. It was his meticulous attention to collecting, holding, packaging and shipping, not to mention his patience with our quarantine and other administrative regulations, that made unescorted transport by jet aircraft eventually successful. The successful shipment left Wellington on 15 April 1961, in a highly insulated container designed for larvae only, utilizing cool, water-logged peat moss. Of the 54 larvae sent in this shipment, 44 pupated and 40 adults emerged, the last on 21 May, to launch the ERC colony.

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The ten degree temperature difference between the natural habitat of *Opifex* and Vero Beach led us to start all colonizing work in constant-temperature rooms which could be kept cool. The work was begun at 12°–15°, but we soon learned that rearing at 25°–27° was quite satisfactory and much easier.

Mated females were kept in standard 12in x 9in x 8in cages and larval rearing pans were white enamel and 16in x 8in x 2in. Pupae were transferred to a large enamelled pan, 18in x 18in x 3in, in a mating or male cage which was 4ft x 4ft x 4ft. Here the emerging females were soon inseminated by the males, which spent most of their time on the water, as described below.

Ovulation and Oviposition

Opifex fuscus is autogenous—i.e., it will mature an initial egg batch without a blood meal. At 20° egg-laying started 6 days after emergence and continued over several days until 75–90 eggs had been laid. The females took blood only after the autogenous eggs had been laid.

The eggs were laid singly and attached to various surfaces. The females preferred to lay eggs under water and on rough substrates, although they oviposited on any moist surface present. Wet cheesecloth was the oviposition substrate finally settled upon for the colony. When laying on this the females walked along laying eggs at four to five second intervals, feeling for the crevices in the mesh with their flexuous abdomens before laying each egg.

Pads of cheesecloth (2in x 2in x 1in) rolled tight and soaked in water were the best oviposition media. They were placed around the edges of the pupal pan and elevated on inverted dishes so that they were roughly half in water and half out. The eggs were tucked quite deeply into the crevices of the mesh, usually in water.

The Egg Stage

Description of the Egg

The eggs are about .3mm x .5mm, rather flat on the ventral surface, and vary from brown to almost black. The shells are transparent enough to permit determination of viability by transmitted light.

The flattened ventral surface of the egg is characterized by protrusions, over the posterior half, which are covered with a gelatinous glue. As a consequence these eggs are not easily washed from the cheesecloth laying pledgets, so are stored *in situ* in petri dishes.

Incubation, Viability and Storage

The fertility of the initial egg batches varied from 40% to 90%, indicating unsatisfactory mating conditions. It was soon found that holding female pupae at 12°–15° while males were held at 25°–27° insured males old enough to mate when the female pupae were brought from cold storage to 25° in the male cage. This immediately increased the number of matings and the percentage of viability in the resulting eggs. By 20 June, second generation adults were being added to the colony.

The incubation period at 25° was approximately 72 hours. During this critical period the substrate was kept continuously saturated. After three days the wet cheesecloth pledgets were laid out on paper towelling for air drying at room temperature. After two or three days, the 2in x 2in pledgets were ready for storage in petri dishes at 8°–10° in either a porcelain or plastic vegetable crisper.

Although rigid experimentation was not possible under these conditions, rough data on storage of eggs are given in Table I. The usual humidity balance between dessication and fungus infection was encountered and precise temperature did not seem as important to survival. With some refinement of methods one might expect average egg survival in storage up to three months and maximum survival about six months.

Egg Hatching

All the eggs we watched hatching differed in no discernible way from other mosquitoes. The larvae leave the egg in the normal mosquito fashion and not tail first as described and figured by Kirk (1923).

Whether eggs remain in water continuously or are stored on cloth pledgets and then flooded, their hatching is quite erratic. They do not respond well to oxygen reduction by replacement with nitrogen (Horsfall, *et al,* 1958), a technique used regularly in this laboratory to achieve synchronized hatches of all *Aedes* and *Psorophora* mosquitoes. For best results with a colony, eggs may be flooded with either fresh or 75% sea water for 4–5 hours and the unhatched ones (i.e., the pledget) returned to storage. Eggs flooded even overnight, if unhatched can be placed back in storage, undamaged, for later use.

THE LARVAL STAGE

Duration

The larval stage varies from 10 to 30 or more days, depending on rearing temperature. In a group of 40 larvae, hatched together and reared in one pan at 27 ± 1°, larval life varied from 11 to 17 days. At 15 ± 1°, the shortest larval period was 23 days. Table II shows the duration of all stages for the 40 abovementioned larvae.

Larval Coloration

First instar larvae are pigmented when hatched from the egg and are immediately very active. The larvae are greyish-black until they reach the prepupal state. Two or three days before pupation, the thorax becomes bluish-green; this is the prepupal stage when active feeding progressively diminishes. Individual larvae when blue-green can be isolated in clean 75% sea water with no further feeding and they will pupate in one to three days.

Larval Development

This rock-pool mosquito can be considered a special type of flood-water mosquito, since its eggs are laid on a moist substrate and can withstand considerable drying for weeks or months, provided it is cold. When embryonic development is completed, the eggs may hatch or they may be dormant in either a flooded or a simply moist situation. This brings about unsynchronized " broods " in the laboratory and may do likewise in nature. The larvae develop slowly and the pupation interval is prolonged.

Several combinations of foods, temperatures, water salinities, and crowding conditions were tried. The best results were obtained at 27° and in 75% sea water. Crowding proceeded from about 400 in a nursery bowl (6in diameter) at hatching to 75 per pan (16in x 8in x 2in) beyond the second instar. At 27°, the feeding schedule yielding best results was the following:

Day 1 Hatch 300–500 eggs in 6in bowl with 75% sea water.
Feed 50mg liver, 50mg yeast, 1 unground dog-food pellet* (40–50mg).

Day 2 No food.

Day 3 No food. Larvae now 2nd instars.

Day 4 Pour into regular pan (16in x 8in x 2in).
Feed 50mg liver, 50mg yeast.

Day 5, 6 Feed 50mg liver, 100mg ground dog food.

Day 7, 8 No food. Larvae moulting into 3rd instar.

Day 9 Separate 3rd instar larvae, 75 per pan.
Feed 50mg liver, 50mg rabbit food†, 50mg ground dog food.

Day 10, 11 Feed 50mg liver, 50mg rabbit food, 50mg ground dog food.

Day 12-17 Feed daily 50mg rabbit food, 50mg ground dog food.

Day 18 Stop feeding. Concentrate stragglers in one pan.

This regime should yield maximum-sized adults with as synchronized and short a pupation interval as can be achieved. The larval period should approximate 15 days and all pupation should occur within an 8-day interval.

Larval Behaviour

The larvae normally spend over half their time on the bottom of the rearing pan. They feed mostly by scraping food off the bottom (hence food should be wetted before introduction to rearing pans) but they also hang at the surface and obtain suspended particles of food by straining water through the mouth brushes. Normal wiggling movements are rather slow, but if disturbed they move very rapidly. They like to have a stone or dark object to retreat under.

We found no evidence of carnivorous or cannibalistic behaviour, as reported by Kirk (1923). As in many other mosquito species, the larvae were to some extent scavengers on dead animals, however.

The Pupal Stage

Duration

The duration of the pupal stage was 72 hours at 27°, 96–105 hours at 20°, and 12 days at 12°. These data were for pupae resulting from adequate larval diets.

Attempts were made to synchronize emergences by retarding early pupae in cold water. Pupae transferred from 27° to 12° immediately after pupation showed about 10% mortality, but if transferred 3 to 6 hours after pupation they all survived. Synchronized emergences brought about in this manner were a great help to the accumulation of equal-aged samples of adults for biochemical analyses.

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* "Gaines Dog Chow" was used.

† "Purina" brand was used.

Pupal Behaviour

Pupal behaviour cannot be discussed independently of the adult male. The latter spends most of his time on the water surface hunting for pupae. (See below.) Since it is to the advantage of the pupa not to be caught until on the verge of emergence, its behaviour seems to be altogether adapted to avoidance of pursuing males.

Pupae were found to spend their time mostly resting on the bottom or moving about under water. They avoided the surface except to pop there one or two seconds, returning to the bottom again, where they often came to rest on their sides with every appearance of being dead. Gradually, and without kicking, the dorsum of the thorax would right itself so that the curved abdomen and paddles were resting on the bottom. Pupae do not rise to the surface automatically, as other species do; a strong kick, or push, against the bottom sends them to the surface for a quick gasp of air. They are apparently in complete equilibrium with the water, possibly because the air bubble they carry is so small in comparison to body weight. This bubble may also shift its position when the pupae are tumbling, thus accounting for the gradual righting of the body on the bottom after having surfaced.

When adult males were in pursuit of pupae in a large pan, the latter would swim 8 to 10 inches either on their side or with a tumbling up-and-down movement before quickly surfacing, demonstrating an avoidance reaction to shadow or movement on the water surface. Young pupae, with chitin not yet hardened, were often injured when males grasped them with their fore tarsal claws. These injured pupae would usually kick on their sides at the surface or at the bottom and die, sometimes 24 to 48 hours later.

The change in surfacing behaviour just before emergence was shown clearly when sample timings were made on pupae of different ages when no adult males were on the water (Table III). Pupae less than 72 hours old spent less than 13% of their time at the surface. The one close to emergence was at the surface 87% of the time, in spells as long as 16 minutes. Soon after these long periods at the surface begin, a shiny film of air starts collecting between the cuticle and the pre-adult. This is the time when the male can quickly insert the sharp-pointed pair of dististyles into the dorsal saddle groove, after capturing the pupa with its powerful forelegs and tarsal claws.

THE ADULT STAGE

Emergence and Mating

Both male and female *Opifex* can emerge from the pupal skin unassisted by adult males, but more of both sexes are successful when a male is holding the pupal case and thus assuring that the emerging mosquito will not capsize. When the male attaches his dististyles and part of both basistyles, he always does so at the dorsal fission line of the saddle-shaped declivity of the pupa's thorax. The frenzied commotion of capture—i.e., the struggle before attachment of the male's genitalia to the pupa's thorax, may attract other males which often join in the melee and often cause the pupa to escape.

When the adult begins to emerge, the male quickly inserts the entire genitalia and eighth abdominal segment into the thoracic region of the pupa. As the adult emerges, the male appresses his genitalia to the lateral side of the abdomen as it slowly advances upwards with peristaltic movements. When the cerci of the emerging female reach close to the male's genitalia, he rapidly effects a connection and immediately runs for objects on the side of the bowl or pan on which he can climb, dragging the female, dangling in a head-down position. She hangs motionless except for a rhythmic pumping of the abdomen, connection lasting 10 to 20 minutes.

If the emerging adult turns out to be a male, such identity is not discerned until the moment the two male genitalia make contact. Then the older male runs away quickly and often attacks other males by trying to pinch them with his dististyles, or else he immediately tries to capture another pupa.

Early in the colonization attempt it was decided to try artificial mating (McDaniels and Horsfall, 1957) in case normal mating was unsuccessful. The first attempt succeeded. A 19-hour old male and a 14-hour old female stayed in copula first two minutes, then three minutes, and after an 11-minute interval, another two minutes. At 21 hours of age the male was dissected. Great quantities of granular fat were immediately revealed in the abdomen (cf. below under adult nutrition). Compared to normal unmated males of other species, the accessory glands were very small and slender, indicating that copulation had drained off seminal fluid. However, the seminal vesicles were not depleted. These vesicles are separated, as in *Culiseta inornata* (Williston) (Lum, 1961). On dissection when 16 hours old, the female had two of its three large, spherical spermathecae filled with sperm, and some could still be seen in the bursa.

Male Behaviour

Post-emergence sexual maturation in *Opifex* males is rapid. The 15–24 hours for terminalia to rotate 180° reported by Marks (1958) must have been at a low temperature. In our observations, rotation of terminalia at 25° began within minutes of emergence, and was seen to reach 45° in less than half an hour. All six males watched at this temperature showed rotation to 45° within an hour and to 90° within three hours. Two of them retained at this temperature reached 160° of rotation in six hours and 180° in eight hours. Maturity (rotation >135°) must then be reached at about 5 to 6 hours at 25°. At this temperature it is reached by 75% of *Aedes taeniorhynchus* in 23 hours and by 95% only in 33 hours (Provost, *et al*, 1961). Ability to copulate successfully is therefore reached very early indeed in *Opifex* males. Nevertheless, males under 6 hours of age were observed to rest only; they could not be induced to chase pupae or spar with other males, the two main activities of older males.

Male *Opifex* spend a great deal of time during the day on the water surface, pursuing pupae and sparring among themselves. They walk, run, or skate on the surface and frequently hop. These hops of 2 to 4 inches would seem to involve wing action, but they are so fast that wing motion cannot be detected.

Pursuing and grappling with pupae is very unique behaviour in *Opifex* males. The role of vision in the pupal hunting habit is certainly paramount. Thus, the response of males to pupae swimming beneath the surface was exhibited only when the bottom of the container was light in colour, providing high contrast to accentuate pupal movements. When the substrate was dark, even light green, the chasing response was not elicited. Males were attracted to the water surface by contrasting dark forms moving against a light background, and once on the water both movement and vibration became orientating stimuli.

The expanding ripples created by pupae when surfacing constitute a fast orientation stimulus. The males immediately orient themselves crosswise to such ripples, facing the centre or origin. The reaction was brought about instantaneously when small air bubbles were released under water or when the water surface was touched with a pencil point. The long middle tarsi would quickly be orientated lengthwise of the wavelets, reproducing quite accurately the arc of the moving ripple. These are the tarsi which also do most of the sculling when the males are swimming or walking on the water surface.

In the absence of tell-tale ripples, males pursue pupae visually. Movement just under the surface seems to excite them most. For this reason pupae of other species (*Aedes, Deinocerites, Culex, Psorophora*) did not disturb them very much, as they were usually motionless at the surface or moving straight up and down when disturbed. The *Opifex* males did nevertheless pursue these exotic pupae and tried to grasp them. Recognition, as in the case of sex, appeared to be largely a matter of feeling with the tarsi and reaction to movements of the body parts.

Males have been seen attracted to pupal skins or to drowning and floating adults. They occasionally fought over a pupal skin, as they often did over pupae. Whether olfaction is involved in such reactions to immobile things was not ascertainable by observation.

Grasping pupae is accomplished initially with the powerful fore tarsal claws. The male's head is usually submerged when this is being accomplished and a film of air surrounds the submerged head and legs. Curved hairs protruding over the eyes capture a large bubble of air before immersion. In ordinary pursuing activities, however, the head is kept above water.

Fighting among males, or tarsal sparring, occupies these energetic males almost as much as chasing pupae. They will often overlook pupae while engaging in this fighting or playing. Here again their sensitiveness to surface vibrations is notable. The males appear to signal one another by vibrating their legs on the water; at least other males seem to respond to such wave signals. No exhaustive study was made of inter-male behaviour, but it is certain that this would be an excellent subject for study.

Female Behaviour

Females which have recently been separated from their first mates were often remated by the same or another male before they could fly off the water. These unions were of shorter duration than the first mating. A few males did copulate with 24-hour old females that flew near the water, making short, flight-like jumps to capture them. Since new females are bound to stay on or close to the water, it must be that nearly all females are mated before they are 24-hours old, whether or not attended by a male at emergence. In this connection it is notable that in two summers of field observation Kirk (1923) never saw a male capture an already emerged female, although he observed this in the laboratory, as we did.

In these laboratory studies, at least, females usually refused to bite man spontaneously, but they could be induced to bite by blowing into the cage while a hand was held inside. They did a lot of probing and took 5 to 12 minutes to fill up on blood.

Adult Nutrition

Both sexes were seen to feed at the sugar-water pads provided for them. To what extent carbohydrate feeding occurs in nature is not known but worth investigating since these mosquitoes reach adulthood with a very considerable store of energy reserves and may not require much adult feeding.

Opifex at emergence are remarkably fat. Biochemical analyses by Dr E. Van Handel of this laboratory showed that both males and females emerged with two to three times the amount of lipid found in newly-emerged salt-marsh mosquitoes, *Aedes sollicitans* and *A. taeniorhynchus.* Their stores of sugar and glycogen at emergence, however, were approximately as in these *Aedes.*

Pupae of *Opifex*, 48 to 96 hours old within that stage, contained much more fat even than the newly-emerged adults. This again points to the interest which must attach to nutritional studies of this strange mosquito.

Discussion

Kirk (1923) was in the main correct in his descriptions of this mosquito's unusual behaviour, but certain of his interpretations need to be reassessed in the light of our observations and experiments under more controlled and elaborate laboratory circumstances. It must first be noted that, although not given, it is clear that his observations were mostly at colder temperatures than ours. This, of course, greatly affected any development rate he touched upon, whether egg, embryonic, larval, or other. But it was particularly in the events at emergence and mating that our respective observations disagree.

He observed, as we did, that pupae spend a lot of time underwater and are adept at eluding capture when immature. We could not confirm, however, that males used only their anal forceps in capturing pupae. They use their great tarsal claws in the capture, but then hold on to the captive pupa only with the anal forceps. We failed also to observe anything like the male slitting the puparium to help the imago emerge. In all our numerous observations the opening of the puparium along the thoracic crest occurred unaided. The male did, however, quickly insert his abdomen, as observed by Kirk. And, finally, we found no evidence that males singled out female pupae for attention. In all other aspects of emergence and mating our observations conformed or extended Kirk's.

The oviposition habits of *Opifex* were well described by Kirk. His report that eggs are laid under water and can live a long time in or out of water, hatching erratically, has been abundantly corroborated. It is difficult, however, to understand what peculiar observational circumstances led him to believe that larvae emerge from the egg tail first. We looked for this assiduously and could find nothing but normal mosquito eclosion.

In the matter of precocious sexual behaviour we find our final failure to corroborate Kirk's observation. He stated that the male " does not commence hunting for pupae immediately on emergence from the puparium, but may do so within ten minutes, and usually does so within twenty ". We found that males did not hunt pupae until 6–8 hours old, and then only half-heartedly. Continuous hunting occurred only in males 24 hours of age or older. Minimum age at copulation was 6 hours, and age at first copulation was seldom under 12 hours. As in other mosquito species, sexual maturity is established by adequate hardening of the cuticle on which is superimposed rotation of the terminalia. The latter process is, however, faster in *Opifex* than in any other species we have studied. The *Opifex* male is certainly precocious, but not to the extent implied in Kirk's report.

SUMMARY

Live *Opifex fuscus* were shipped from New Zealand to Vero Beach, Florida, where a colony was established at the Entomological Research Center.

Oviposition. Eggs are laid singly, mostly underwater, and attached to rough surfaces. Pads of cheesecloth rolled tight and soaked in water make good oviposition media.

Eggs. High egg fertility was achieved by retaining female pupae in a cold box (12°–15°) while male pupae developed at 25°–27°. Males sufficiently old then attended female pupae, later introduced to their pan, to assure mating at emergence. The egg incubation period at 25° is 72 hours. Eggs on pledgets of cheesecloth can be kept in a cold box several months. Eggs hatch erratically, no matter how treated.

Larvae. The larval period at 27° extends from 11 to 17 days. The pupation interval is characteristically extended. Larvae develop well in 75% sea water on a diet of yeast, powdered liver, dog-food pellets, and rabbit food. They feed mostly on the bottom and are not carnivorous.

Pupae. At 27° the pupal stage lasts 72 hours. Young pupae spend nearly all their time on the bottom. As the time for emergence nears, they become like pupae of other species and stay at the surface, where they are attended by the male adults.

Emergence and Mating. Both sexes can emerge successfully without male attendance. Normally, males capture pupae and as soon as the pupal thorax splits they insert the entire genitalia and eighth abdominal segment. Coitus is accomplished as soon as the cerci of the emerging female reach the male's genitalia, before the actual shedding of the skin. Males cannot distinguish sex until genital contact has been made. Coitus lasts 10–20 minutes.

Male Behaviour. Males spend most of their time on the water, pursuing pupae and fighting (or playing ?) with one another. Although post-emergence sexual maturation is rapid, this behaviour is seldom seen before they are 12 hours old. The pursuit and capture of pupae is mediated primarily by vision, although vibrations of the water surface also serve as stimuli. Pupae of other species are pursued. The males mate with emerging or recently emerged female *Opifex*.

Female Behaviour. Newly-emerged females stay on or near the water. If not mated at emergence by an attending male, they almost always are soon after emergence. Females did not bite man spontaneously, but could be induced to do so.

Adult Nutrition. Both sexes fed to some extent on sugar-water pads. However, they are so remarkably fat at emergence that they can live several weeks without nourishment.

This mosquito has not been mass-reared. The rearing recommendations given here are based on preliminary experience with 12 generations. The species is adaptable to mass colonization and offers unique study values in comparative behaviour, nutrition, and energetics.

TABLE I

Viability of *Opifex* Eggs Stored Under Various Conditions for Variable Lengths of Time.

Group	Age in Days, at Flooding	Conditions Temp. (°C.)	Moisture	Eggs No. Flooded	No. Hatched	% Hatched
1	9	25	medium	300	275	92
2	33	8–10	medium	500	410	82
3	59	8–10	medium	200	136	68
4	64	25	low	1000	0	0
5	66	8–10	medium	600	169	28
6	76	25	medium	500	147	29
7	101	8–10	high	*75	0	0
8	115	8–10	high	100	25	25
9	128	8–10	high	400	102	26
10	135	8–10	medium	200	25	13
11	141	8–10	medium	300	9	3
12	147	8–10	medium	*100	0	0

* Fungus infection.

TABLE II

Duration of Stages for 40 Larvae of *Opifex* hatched and reared together at 27°.

	Days After Hatching
First instar larva	1–2
Second instar larva	3–4
Third instar larva	4–6
Fourth instar larva	7–17
Pupa	11–20
Adult	14+

TABLE III

Time Spent at Surface as a Function of Pupal Age. No Adult Males on Water Surface.

Age (hours)	Sex	Time Spent (seconds) Total	Surf.	% Surf.	Longest Unchanged Positions (seconds) At Surface	At Bottom
1–4	?	481	55	11.4	12– 9– 4– 4–4	68– 58– 40– 32–32
24	♂	865	107	12.6	30– 12– 8– 5–5	190–138–125–120
48	♀	691	30	4.3	6– 4– 3– 3–2	70– 65– 54– 54–50
72	♂	1771	1555	87.3	990–330–60–60	45– 35– 35– 15–15

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