Aspects of the biology of *Opifex fuscus* Hutton (Diptera : Culicidae)

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Synopsis

Aspects of the biology of *Opifex fuscus*, a mosquito that breeds in pools of the spray zone on the coast of New Zealand, are described, and the way in which these enable the mosquito to use these temporary pools, in which physical conditions fluctuate irregularly and rapidly, is discussed.

Introduction

The mosquito *Opifex fuscus* Hutton breeds in pools above high water along New Zealand's coasts. Aspects of the biology of *O. fuscus* were investigated during the course of a study of the ecology of pools in the spray zone (the region of the shore above mean high-water neap but continually influenced by spray and splashing) at Taylors Mistake near Christchurch and at Kaikoura, 100 miles north of Christchurch, during 1961 (McGregor, 1964). No pools at Taylors Mistake exceeded 1000 litres in volume but most of those at Kaikoura had volumes of the order of 10,000 litres. Some of the smallest pools were filled for only a few days once or twice during the year. Larvae of *O. fuscus* were not usually found in such ephemeral pools but were not restricted to permanent pools. At Taylors Mistake some pools, in which large numbers of larvae bred, dried up several times during the year.

The blue-green alga *Enteromorpha* grew in many of the pools. *Enteromorpha* was most abundant at Taylors Mistake in May, August and September and scarce or absent in June, July, November and December. Other genera of algae found associated with *O. fuscus* included *Oscillatoria* and *Lyngbia* in hyperhaline pools, and *Chaetomorpha*, *Cladophora*, *Rhizoclonium* and *Rhodochorton* in conditions that more closely approached those of sea water.

The orange copepod *Tigriopsus fulvus* (Fischer) was present, often in huge numbers, in pools containing larvae of *O. fuscus*. Nematodes, amphipods and larvae of the dipteran *Ephydrella novaezealandiae* Tonnoir & Malloch were common, and the littorinid Gastropods *Melaraphe cincta* (Quoy & Gaimard) and *M. oliveri* Finlay were found in or around many pools.

Mating Behaviour

The peculiar mating behaviour of *O. fuscus* has been described by Kirk (1923). During spring, summer and early autumn large numbers of adults, predominantly but not exclusively males, congregated on the water surfaces of pools. An estimated nine to eleven thousand adults were on the surface of one large pool at Kaikoura on 3rd March. Males converged on pupae as they rose to the surface, and there was often vigorous competition between ten or twelve males for the possession of a single pupa. If a male pupa was captured it was released within about 5 seconds of capture.

Emergence of the young female imago began almost immediately after capture and was usually completed in 5–30 minutes. Connection lasted only a few minutes in some pairs but up to 50 minutes in others. Establishment of connection between

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two free adults was never seen. As soon as connection was broken the male would fly off, but the female usually rested for several minutes. In laboratory populations females emerged unassisted by males, although higher mortality of female pupae suggested that their facility for unaided emergence may not equal that of males. The sex ratio in populations of *O. fuscus* did not appear to depart significantly from unity.

The reduction in time between maturation of females and their fertilisation to an absolute minimum, and the competition between males for females would increase the reproductive efficiency within populations. Two important causes of mortality of larvae and pupae of *O. fuscus* are the drying up of pools and the washing out of pools by rough seas. In a coastal-living species it seems possible also that precocious mating would reduce the likelihood of any females remaining unmated in the event of dispersal by wind. The precocious mating behaviour of *O. fuscus* is an adaptation towards ensuring efficient fertilisation of those females that do develop to maturity.

OVIPOSITION

Females of *Opifex fuscus* deposit their eggs around pool margins in a damp zone, which reaches from 1–5 cm. above the water surface. Small cracks and crannies in rock were favoured, but eggs were laid on pebbles, shells, pieces of wood and filaments of algae, especially when the density of the adult population was high, and there was keen competition for egg-laying sites.

During oviposition the female arches her abdomen under her thorax and oviposition is preceded by rapid movement of the antennae and proboscis over the surface of the substrate. A slow relaxation of the abdomen is visible as the egg is expelled. Six to ten eggs may be laid in quick succession at one site. The firmness with which eggs adhere to the substrate is variable, and some eggs, especially those laid on smooth surfaces on which the area of attachment is small, are easily dislodged. It is common to find eggs floating on the surface of pools or lying loosely on the mud and sand of pools that have dried up.

HATCHING MECHANISMS

Gjullin *et al.* (1941) and Judson (1960) have demonstrated that the hatching of eggs of various species of aedine mosquitoes is induced by lowering the oxygen tension in the floating medium.

When eggs of *Opifex fuscus* collected at Taylors Mistake were dried at room temperature in the laboratory for 3 days and then submerged in sea water or fresh water, almost all hatched within 12 hours. Eggs from the same source, which were submerged in sea water saturated with oxygen by continuously pumping compressed air through the water, did not hatch. Twelve of twenty eggs that were dried at room temperature for 6 months hatched within 24 hours of being flooded with untreated sea water. The remaining eight failed to hatch.

These results are consistent with the theory that a decrease in the oxygen tension of the flooding medium provides a stimulus for hatching, as it does for the eggs of other aedine mosquitoes. As many of the pools in which larvae of *O. fuscus* breed are temporary, the ability of eggs to withstand desiccation for at least 6 months enables populations to survive through long periods when pools may be dry. Rapid hatching after flooding ensures that the aquatic stages in the life cycle fully utilise the available water for their growth and maturation.

LARVAL POPULATIONS

Larval populations were sampled by inserting a Perspex rectangular box (volume, 224 cc.), open at both ends, into pools with as little disturbance as possible and then quickly sliding doors over each end of the box, thereby enclosing within it larvae from a constant volume of water. The procedure was repeated several times in each pool, and the mean number of larvae per sample was taken as an approximate index of density.

The level of larval populations within pools fluctuated irregularly. Increases in the density of first instar larvae almost invariably occurred within a day of a rise in water level caused by rain or sea splashing. For example, in Pool C at Taylors Mistake on 11th February, when the pool was nearly dry, the mean figure for first instar larvae per sample was 9, but after rain on 12th and 13th February the pool became filled with water, and the mean number of first instar larvae per sample increased to 102. The mean number of fourth instar larvae per sample decreased from 10 to 1 over the same period. Changes in the volume of water within pools would influence density, but irregular hatching of eggs and an unequal duration of instars would be important factors affecting the relative representation of instars.

In small temporary pools fourth instar larvae and pupae were usually greatly outnumbered by earlier instars, and the life cycle of few individuals proceeded to completion. As the volume of the pools decreased by evaporation, larval densities exceeding one larva per cc. were common, and tremendous wastage of breeding potential resulted from the drying up of such pools.

Larvae were present in pools at Kaikoura, Taylors Mistake and Lyttelton Harbour during the winter months, although numbers were lower than those found in the summer. Washing out of pools during a severe storm almost abolished larval populations at Taylors Mistake during July. On July 22nd only four larvae could be found, all in one pool, but by 16th August first instar larvae were numerous in all pools. The mean number of larvae per volume sample in Pool B at Taylors Mistake on 5th September was: first instar, 198; second instar, 30; third instar, 6; fourth instar, 6.

PUPAL AND ADULT NUMBERS

The number of pupae in pools at Taylors Mistake were counted directly, and counts of the number of adults upon pool surfaces gave an index of the adult population. In pools at Taylors Mistake the total numbers of pupae fluctuated from 227 on 20th February to 38 on 3rd March, 481 on 22nd March and 141 on 29th March. By 7th May there were only three pupae, and no further pupae were seen at Taylors Mistake till 2nd October. Counts of adults showed fluctuations roughly parallel to those of pupae, with an irregular decline from a peak of 487 on 8th February to 134 on 3rd March, 308 on 22nd March and 129 on 29th March. Seven adults were seen on 29th May, but from that date none were seen at Taylors Mistake until mid-October.

GROWTH RATES

First instar larvae collected at Taylors Mistake were reared individually in test tubes containing 25 ml. sea water, which was changed every second day. Equal volumes of commercial fish food or Loefflers dehydrated blood serum were added as food to each tube after every water change.

Groups of ten larvae were reared at 13° C. ± 1° C., or 25° C. ± 2° C., and in complete darkness and normal day-lengths at room temperature (Table I).

TABLE I.—*Growth rates of* Opifex fuscus *larvae and pupae*

	Mean time (days)			
	Instar II	Instar III	Instar IV	Pupae
25° C.	1·3	1·2	3·7	1·2
13° C.	3·8	4·1	17·3	3·3
Room temperature*				
Normal day-lengths . .	4·2	2·3	14·1	3·2
Complete darkness . .	4·2	2·3	18·4	3·3

* Range: 12–19° C., mean over 30 days 16·2° C. (taken during the experiment).

Under all the conditions the stage of longest duration was the fourth instar. As Huffaker (1944) has noted, the growth of the fourth instar involves by far the greatest increase in mass, as well as basic tissue transformation. The greater length of the fourth instar in complete darkness than in normal days may have been due to the influence of the absence of light on the solutions in which the larva were reared (for example, reduction of the number of micro-organisms available as food for larvae (Bates, 1949)), rather than to some direct effect of light on the growth processes of larvae. Jobling (1937) concluded that *Aedes aegypti* (L.), *Culex pipiens* L. and *C. fatigans* Wiedemann grow equally well in the presence or absence of light.

When ten individuals of each larval instar were placed in a refrigerator (3° C. ± 2° C.), all first and second instar larvae were dead within 5 days, but fourth instar larvae survived, without moulting, for two months. That larvae could tolerate temperatures higher than 25° C., at least for short periods, was apparent from field observations that revealed temperatures as high as 36° C. in pools containing larvae of *O. fuscus*.

Larvae of *Opifex fuscus* exhibit environmentally controlled dimorphism, some larvae having only simple hairs in their mouth-brushes and others having mouth-brushes that contain pectinate bristles (McGregor, 1963), but there were no apparent differences in the growth rates of the two forms.

SALINITY TOLERANCE

From field observations it was obvious that larvae of *Opifex fuscus* had a wide salinity tolerance. The maximum salinity recorded from pools containing larvae was 90‰, whereas the minimum was 0·4‰, *i.e.* virtually fresh water. Larvae of *O. fuscus* have been collected from a fresh water stream (Dumbleton, 1962).

Larvae collected at Taylors Mistake were placed in individual tubes containing water of the desired salinity. Solutions used were distilled water, tap water, sea water diluted to 3‰ with tap water, sea water diluted to 18‰ with tap water and artificial sea water prepared from a stock solution having the following composition: KCl (2·4 M.), 1·8 ml.; $CaCl_2$ (1·6 M.), 2·8 ml.; $MgCl_2$ (1·6 M.), 14·5 ml.; NaCl (2·4 M.), 80·9 ml.

The concentration of this solution in respect to the major cations was four times that of sea water. Any lower concentration required was produced by dilution with M/400 $NaHCO_3$.

The water in the tubes was changed daily, and equal volumes of commercial fish food were added to each tube after every water change. The survival of larvae in each solution, and after transference from one solution to another, was recorded. When a larva was transferred from one solution to another, it was pipetted, with as little liquid as possible, from the initial solution to one of the desired concentration, in which it was left for several minutes before being finally moved to another tube containing a similar solution. Ten larvae were used in each experiment.

All instars survived and developed in distilled water, tap water, sea water diluted to 3‰ and 18‰, normal sea water and artificial sea water (35·5‰). The addition of fish food to distilled water would have supplied some salts, but nevertheless larvae of *O. fuscus* are remarkably tolerant of negligible salinities. No larvae survived transference from normal sea water to distilled water, but three out of ten third instar larvae survived a change in the opposite direction. All larvae survived all possible combinations of changes between tap water and water of salinity 3‰, 18‰ and 35‰. Six of ten first instar larvae, and four of ten second instar larvae, died within 24 hours of transference from artificial sea water (35‰) to artificial sea water (70‰). All of 20 third and fourth instar larvae survived a similar change. Two of the surviving first instar larvae died in their second instar, but all other larvae completed their life cycle at 70‰. Ten larvae of each instar were transferred from artificial sea water

(35‰) to artificial sea water (105‰), but only one, a fourth instar, survived and pupated.

Forty first instar larvae were reared in a dish containing normal sea water and commercial fish food. As evaporation gradually raised salinity, counts of larvae and periodic determinations of salinity were made. Ten larvae had died when salinity had reached 95‰, and moulting and pupation had ceased when the salinity had reached 130‰, 36 days from the beginning of the experiment. Adults emerged from all six pupae present when salinity was 130‰. The last of the 12 larvae that were surviving at 130‰ had died when the salinity had risen to approximately 165‰.

Discussion

The pools in the coastal spray zone form difficult environments for plants and animals. Physical conditions such as salinity and temperature fluctuate irregularly, and often rapidly (McGregor, 1964), and for successful colonisation plants and animals must be able not only to withstand these fluctuations but also to survive desiccation and the flushing out of pools at any time during a year. The biology of *O. fuscus* shows many adaptations to this variable and temporary environment. The precocity of female pupae and the vigorous competition between adult males for mature female pupae ensure efficient fertilisation of those females that do develop to sexual maturity as well as minimising the time between the maturation of the females and their fertilisation. High reproductive efficiency is important to species in which there is the possibility of high mortality in the immature stages.

It appears that an essential criterion for oviposition sites is that they be moist. Such a condition would reduce the possibility of eggs being laid while evaporation rates were high and pools likely to be decreasing in volume. Eggs laid in the moist zone above water level will hatch only when submerged, that is, only when there is an increase in the volume of water within a pool and thus an increased possibility for successful development of larvae and pupae. The wide temperature and salinity tolerances of the larvae would enable at least some to survive most of the variations in water conditions in pools in the coastal spray zone of New Zealand.

The high densities reached by populations of *O. fuscus* at Taylors Mistake and Kaikoura may be a reflection not only of adequate adaptation to the physical conditions of the environment but also to the absence of competing species. *Aedes* (*Halaedes*) *australis* (Erichson) has not been found at Kaikoura or Taylors Mistake to date, but 200 miles to the south, in Otago, both *O. fuscus* and *A. australis* breed in the same pools (Nye and McGregor, 1964). In Otago populations of *O. fuscus* are very much smaller than at Taylors Mistake or Kaikoura, and larvae of *O. fuscus* are heavily out-numbered by *A. australis*. Larvae of *O. fuscus* and *A. australis* appear to occupy similar ecological niches: they breed in the same pools; they exhibit similar mouth-brush dimorphism (McGregor, 1963), and an examination of gut contents has not revealed any differences in feeding habits; *O. fuscus* can withstand a range of physical conditions similar to that tolerated by *A. australis* (Woodhill, 1936; O'Gower, 1960). Populations of *O. fuscus* in Otago may be restricted by competition with *A. australis*, and if *A. australis* arrived comparatively recently in New Zealand from Australia (Nye, 1962), some reduction in populations of *O. fuscus* in other parts of New Zealand might be expected if *A. australis* becomes more widely distributed.

Summary

After a general description of the pools of the spray zone on the coast of New Zealand, in which the mosquito, *Opifex fuscus*, breeds, the adaptations it displays to life in these rapidly fluctuating environments are discussed. These are:

1. the way in which rapid and effective mating is ensured by the capture of the mature female pupae by the previously emerged males;

2. the choice of sites for oviposition of such a nature as to reduce the likelihood of the eggs being laid where evaporation rates will be high, and the presence of mechanisms that ensure that the eggs will only hatch after flooding and that the process will then be rapid;
3. the quick rate of growth and the ability of the larvae to tolerate a wide range of salinity and temperature.

Study of the populations of larvae showed a rapid build up of numbers in the spring and summer months that reflects not only successful adaptation to the physical conditions of the environment but also the absence of competing species.

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Book Notice

Animals and plants of the Cenozoic era: some aspects of the faunal and floral history of the last sixty million years. By R. G. Pearson. 8vo. London: Butterworths, 1964. Pp. vii, 236, 36 text-figs. 55*s*. 0*d*.

This book brings together information about the faunal, floral and climatic events of the age of mammals based on the work of botanists, geochemists, geologists and zoologists, presenting topics normally discussed only in specialist publications. It provides for the first time a picture of the subject as a whole.

The work is divided into the following chapters: introduction; the Tertiary sequence in the Paris Basin (pp. 11–18); Tertiary vegetation (pp. 19–52); the Quaternary vegetation (pp. 53–73); the full-, late-, and post-glacial periods (pp. 74–90); isotope dating and further climatology (pp. 91–108); Carnivora (pp. 109–25); Condylarthra and South American ungulates (pp. 126–36); Artiodactyla (pp. 137–56); Perissodactyla (pp. 157–67); proboscideans (pp. 168–74); primates (pp. 175–93); synthesis (pp. 194–200).

Although there are few specific references to insects, the information about the climate and vegetation of the Cenozoic era cannot fail to be of interest to entomologists.

There is a list of references (pp. 201–15) and a twenty-page index of subjects and scientific names.