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The biology of a tropical mayfly *Povilla adusta* NAVAS (Ephemeroptera, Polymitarcidae) with special reference to the lunar rhythm of emergence

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INTRODUCTION

There are relatively few papers which deal with the biology of Ephemeroptera and most of these refer to species from temperate regions. GILLIES (1954) has described the biology of the specialised genus *Prosopistoma* in Tanganyika, but apart from this paper our knowledge of the biology of tropical mayflies rests almost entirely on references in the taxonomic literature. Several of these references concern the genus *Povilla* and the present study was undertaken with the object of augmenting the knowledge of the sole African representative of the genus, *Povilla adusta* NAVAS. The biology of this species was first mentioned by ARNDT (1938) who found the larvae living in tunnels in freshwater sponges from lakes in the Belgian Congo. These tunnels were lined with a brownish film which ARNDT suggested might have been produced by the larvae. KIMMINS (1948) refers to larvae of the same species found by Miss R. H. LOWE in Lake Nyasa; Miss LOWE also suspected that the larvae, which were burrowing in the bottoms of wooden boats, produced the papery lining which she observed in the burrows. Since the production of any silk-like substance was unknown in the Ephemeroptera, KIMMINS suggested that this point might repay investigation in the field and BEADLE (1953) showed that the substance is definitely produced by the larvae.

MATERIAL AND METHODS

Most of the material used in this study was obtained at Kaazi (32° 37′ E, 0° 14′ N) which is on the shore of Lake Victoria about twelve miles south-east of Kampala. The shore is here easily accessible by car and is sheltered so that the plants from which larvae were obtained remained relatively undisturbed.

In the margin of the lake there is a profuse growth of *Cyperus denudatus* L. mixed with other aquatic plants; it was found that the larvae of *Povilla* could conveniently be obtained by cutting off the basal twelve inches of dead *Cyperus* stems and taking them back to the laboratory in churns of water. The larvae were usually left in the stems but could easily be extracted if required by splitting the stems. In the laboratory the larvae were kept in tanks full of lake water at room temperature (22-24° C.) the tanks being continuously aerated.

Quantitative samples of adults were taken at Kaazi by a simple method which nevertheless appeared to produce consistent results. A car was parked facing the lake on a small rocky eminence about ten feet above the water and twenty feet away from it. A cotton sheet was then spread on the ground in front of the car and the lights switched on. The mayflies were then picked off the sheet by hand as they arrived. The success of this method may be due partly to the great difficulty with which adult *Povilla* leave the ground, their legs being greatly reduced.

A small amount of material was collected at various other localities in Uganda but none of it was used for experimental purposes.

ASTRONOMICAL INFORMATION

Since *Povilla adusta* has been found to possess both diurnal and lunar rhythms, it is necessary to draw attention to those aspects of the diurnal and lunar cycles which affect conditions on the Equator.

a) *Length of day :*

During 1955 the length of day on the Equator measured between zenith distances of 90° 50′ varied between 12 hrs. 6 mins. and 12 hrs. 8 min., this variation showing no obvious seasonal arrangement.

b) *Times of sunrise and sunset :*

In 1955 and 1956 the times of sunrise and sunset, both measured at a zenith distance of 90° 50′, varied through an annual range of thirty-one minutes, the rate of change being greatest between November and the following February.

c) *Times of moonrise and moonset :*

The times of these phenomena are related to the phase of the moon. At full moon, moonrise occurs at about 1800 hrs. and is delayed by about 50 minutes per day so that at new moon moonrise occurs at about 0600 hrs. There is some variation in the times of these phenomena at a given phase of the moon (for example in 1955 the time of moonrise on the date of full moon varied between 1740 hrs. and 1844 hrs.), but the total duration of moonshine per day is less variable, ranging in 1955 from 11 hrs. 21 mins. to 11 hrs. 37 mins. At new moon, of course, this period is almost entirely during daylight.

d) *Intensity of moonlight :*

The intensity of moonlight rises to a sharp peak at full moon, when it is eight times as great as it is at the quarters.

e) *The synodic month :*

The internal which elapses between successive repetitions of a particular phase of the moon is called a synodic month and is approximately 29 days 12½ hours. The dates on which a particular phase falls may thus be separated by intervals of either 29 or 30 days, the arrangement of these intervals not following any obvious series.

THE EGG

The eggs of *Povilla adusta* are laid in masses which may be found attached to plant material floating at the surface of the water. When freshly laid the eggs from each of the two oviducts adhere in a dense khaki-coloured matrix of the consistency of chewing-gum, but on contact with water the two egg packets swell rapidly and fuse, forming a gelatinous egg-mass about 5 mm. thick and 15-25 mm. long. At either end of the mass there is a bunch of twisted fibrous coils which anchor the mass to any floating object which it meets.

The number of eggs in an egg-mass varies between about one thousand and two thousand five hundred, the larger masses containing the greater number of eggs.

It is estimated that the duration of the egg stage in the field is eleven or twelve days since in the laboratory, where the temperature is three or four degrees cooler than in the lake, development takes twelve to fifteen days. Support for this estimate is provided by the fact that eggs have only been found in the field within two weeks of the previous swarms of adults.

THE LARVA

The external morphology of the full-grown larva has been described by DEMOULIN (1956) so that it will only be necessary to mention features of particular functional significance; the general appearance of the larva is not unlike that of the larva of *Ephemera*.

Almost all of the larval instars of *P. adusta* have in common a number of interesting specialisations, notably the filter-feeding mechanism, the burrowing habit and the faculty of producing silk-like material; all of these attributes are absent from the first two instars, however, and these will not be discussed here.

It has already been mentioned that larvae were obtained from the dead stems of *Cyperus denudatus*. They may be found, however, in almost any material of suitable consistency in all of the large East African lakes which have been examined. A wide range of plant materials, including wooden boats and canoes, have been found to be damaged by the larvae, while they are occasionally found making silken tunnels amongst shell fragments or gravel. The larvae construct their burrows by using the large, heavily sclerotised mandibular tusks which, unlike those of *Ephemera,* point forwards. The burrow is usually constructed so that it runs parallel with the surface of the material in which it is made; when newly bored, the burrow is only slightly longer and wider than the larva, but with use it gradually increases in length and girth. The burrow is lined with a silk-like substance which has been shown by BEADLE (1953) to be produced by the larva. Observations on larvae kept in glass tubes have shown that this material, which is produced by the Malpighian tubules, passes out of the anus as a viscous mass. This is moulded by the mouthparts and is then spread out by smearing movements of the forelegs. Two functions appear to be served by the silken lining. In the first place it provides a foothold for the larva; this is especially important when the larva is feeding since the action of the gills tends to force the larva forwards out of the burrow. Secondly, the lining serves to reduce the lumen of the tube, ensuring that the water current passes through, rather than round, the brushes of filtering setae.

The larva anchors itself in its burrow by means of the last two pairs of legs, both of which are curved dorso-ventrally and bear short peg-like setae on their outer surfaces. It was found that larvae would live satisfactorily in the laboratory in glass tubes of suitable bore. Examination of larvae living in such tubes soon showed that they fed by filtering the water in which they live; a current of water is produced by the action of the six pairs of feathery gills, the water then being filtered through brushes of pinnate setae on the mandibular tusks and forelegs (HARTLAND-ROWE 1953). In this connection it is of interest to note that, whereas in many Ephemeropteran larvae the pairs of gills develop one by one at successive instars, in *Povilla adusta* the mobile gills all develop at the third instar which is the stage at which the larvae commence feeding. IDE (1935) has observed a similar development in the larvae of *Ephoron* which may feed in the same manner as *Povilla.*

Examination of the pinnate setae of a full-grown larva of *Povilla* shows that the pinnae are arranged at intervals of about 8 mu, interlocking with the pinnae of adjacent setae. Thus all the water passing through the filtering brushes is filtered through a mesh of less than 10 mu; this is sufficiently fine to retain most of the suspended and planktonic algae.

It appears from illustrations of larvae of other Polymitarcidae that they possess brushes of setae resembling the filtering brushes of *Povilla* larvae. It would be of great interest to determine whether these forms also feed by filtering water. It would also be desirable to know whether, like *Povilla adusta,* they line their burrows with silk. REAUMUR (1744) remarks that the wall of the mud burrow of *Ephoron virgo* (OLIVIER) is of a finer texture than the surrounding mud and appears to be laid down in an even layer; this perhaps suggests that the mud is mixed with silk.

Unless they are disturbed, the larvae of *Povilla adusta* remain in their burrows throughout the day. Visits to the laboratory during the night showed that they swim actively after dark. Observations were rendered difficult by the great sensitivity of the larvae to nocturnal illumination; the use of an electronic apparatus incorporating a photo-electric cell showed that they would avoid a beam of light which was not strong enough to illuminate them. This apparatus was unfortunately found to respond to the considerable voltage fluctuations in Kampala and its use was therefore discontinued. Observations were eventually made by flashing a light on a tank containing larvae and their burrows;

provided the light was only on for a few seconds, this did not appear to influence the activity of the larvae.

A limited series of observations by this method showed that a considerable proportion of the larvae in a tank swim for extended periods during the night. Larvae have been observed swimming during every half-hour period from 7.30 p. m. to 7.00. a. m., while they have never been seen to swim during daylight unless they had been violently disturbed. A few observations made on larvae kept in darkness for two weeks showed that the rhythm was still apparent and was still in phase with the external daylight cycle.

HARKER (1953) has shown that the larvae of three British species of may-fly show diurnal rhythms of activity, being more active during the night even under conditions of constant darkness. Using *Heptagenia lateralis* (CURTIS) she demonstrated that this rhythm is not endogenous, but is induced in the egg or during early larval life by the daylight cycle. By rearing larvae from the egg in constant darkness, she was able to produce arhythmic larvae; these, when subjected to abnormal light conditions for twenty-four hours and returned to constant darkness, developed a correspondingly abnormal activity rhythm. This suggests a means by which the activity rhythm of *Povilla* larvae may be produced. Also the great sensitivity of the larvae to nocturnal illumination suggests a possible means by which a lunar rhythm might be induced.

Larvae of *Povilla adusta* of all sizes may be found at all times of the year in Lake Victoria and do not show any marked annual variation in numbers. It has been shown (HARTLAND-ROWE 1955) that emergence takes place throughout the year in close relation to the lunar cycle and it was hoped that this might provide a means of estimating the duration of larval life. Random samples of larvae were collected and measured in the hope that the expected polymodal size distribution would indicate the duration of larval life in lunar months. This method was discarded when it was found that no consistent polymodality could be discerned. Attempts at rearing larvae in the laboratory with a view to obtaining a rough estimate of the duration of larval life were also unsuccessful. CORBET's estimate (1957) of a larval life of three or four months is supported by the results of a subsequent attempt at rearing larvae in cages in Lake Victoria; these results suggest that four months is probably the mean duration of the immature stages (including the egg) while a few individuals may develop in three or five months.

THE ADULT

Adults were not seen in the field for more than a year after this study commenced although several had emerged from time to time in the laboratory. These always emerged between dusk and 9 p. m. by which time they were always dead. Visits were accordingly made to Kaazi between these hours and eventually large swarms were encountered both there and elsewhere. The account which follows is incomplete, since the fact that the whole life of the adult is spent in darkness rendered observations difficult.

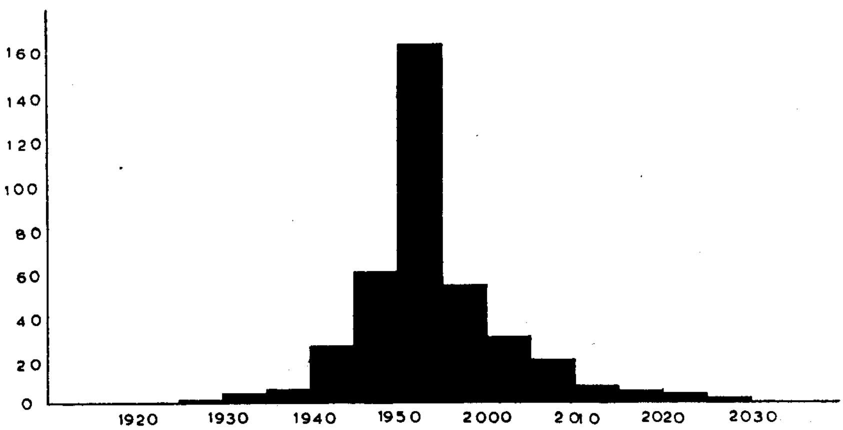

Fig. 1. — Histogram illustrating the relationship between time of day and the number of *Povilla adusta* adults coming to light (15 Aug. 1954).
Abscissa: East African Standard Time.
Ordinate: Number of individuals.

At about 7.30 p. m. the mature larva swims to the surface, remains there for a few seconds and then casts its cuticle. The subimago which is released immediately flies up into the air and within a few minutes, or possibly only a few seconds, the subimaginal cuticle is shed. It is suspected that nuptial swarming of the imagines takes place high in the air, since it is sometimes possible to see large numbers of *Povilla* flying to and fro about thirty or forty feet above the surface of the lake. Adults usually begin to come to light at about 7.30 p.m. and the number of arrivals increases to a maximum by about 7.55 p.m. The numbers then usually decrease until 8.30 p.m. when no new arrivals are seen (Fig. 1); on two occasions a second wave of arrivals has appeared at about 8.20 p.m. decreasing to zero at about 9. p.m.

During August 1954, samples of adults were taken at Kaazi every night for the fortnight spanning 14 August, the date of full moon. The results (Fig. 2) show that the greatest number emerged on the second evening after full moon, while a negligible number appeared before 13 August or after 19 August. During this experiment the greatest number of individuals always arrived at about 7.55 p.m., despite the variation in the position of the moon. Since the life of the adult is only about one hour, the majority of individuals did not live to see the moon on any night after the second evening following full moon.

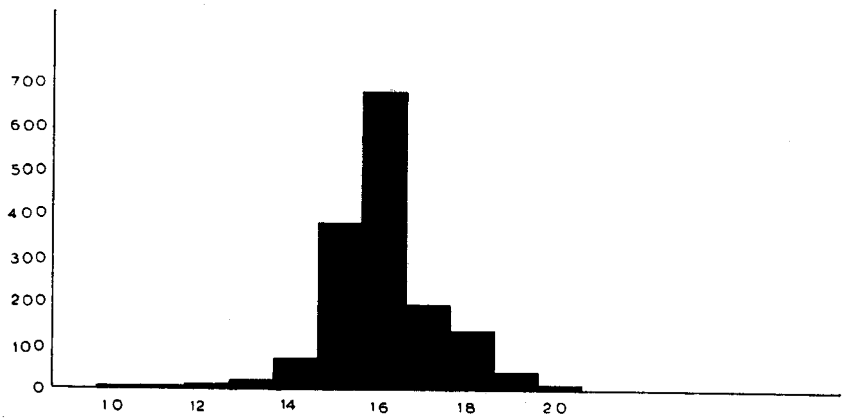

Fig. 2. — Histogram illustrating the relationship between the phases of the moon and the numbers of *Povilla adusta* adults coming to light during the evening. (August 9 to August 24, 1954).

Abscissa: Date in August. (Full moon: 14 August).
Ordinate: Number of individuals.

Examination of the relationship between the dates on which large swarms of *Povilla adusta* have been seen and the phase of the moon shows that on Lake Victoria the dates of swarms are closely grouped round the second evening after full moon, while elsewhere they are more scattered (Fig. 3). This is shown more clearly by Fig. 4 which portrays the distribution of all available records of *Povilla* adults relative to the phase of the moon, each square representing one night at one locality where adults have been seen. One square may thus represent any number of adults from one to an estimated nine thousand (27 May 1956). It is evident that emergence in Lake Victoria is closely related to the phase of the moon; this relationship is retained in laboratory emergences under all experimental conditions. Emergence in the other lakes does not show any clear relationship to the phase of the moon although a Chi-square test does show that emergence in Lake Albert is not random with respect to weeks ($P < 0.05$).

Since mature larvae may be found at all phases of the moon there is clearly a causal relationship between the lunar cycle and the date of

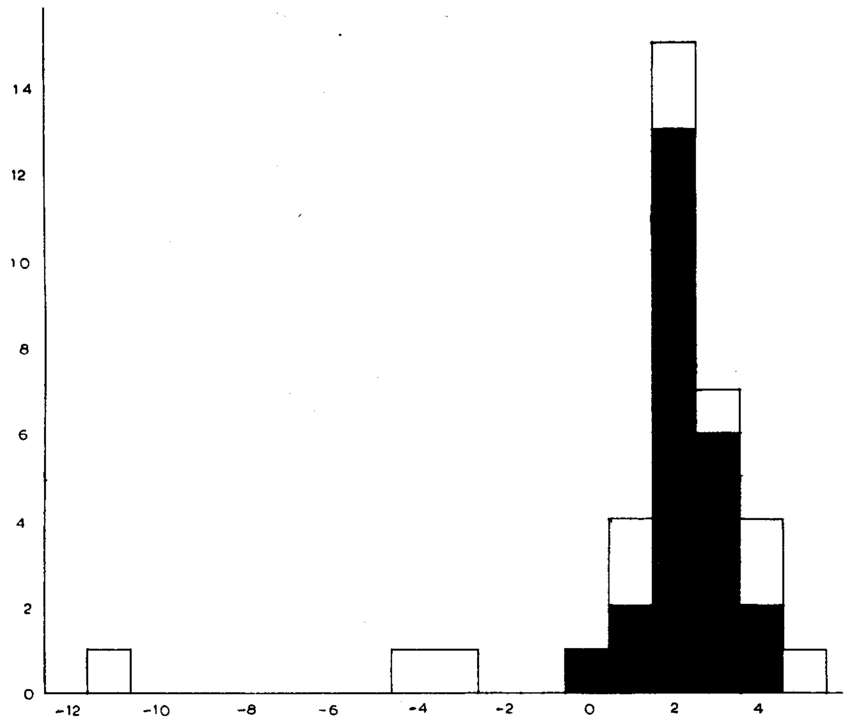

Fig. 3. — Histogram illustrating the relationship between the phase of the moon and the dates on which swarms of *Povilla adusta* have been observed. Black squares refer to Lake Victoria, white ones to other localities.

Abscissa: Number of days after full moon.
Ordinate: Number of swarms.

emergence in Lake Victoria. Of the biotic factors which might influence the larvae, none has been found to possess a lunar rhythm; the physical variables associated with the lunar cycle were therefore considered. Of these factors, those related to the light of the moon were considered first, because their effects on the environment are more profound than other physical factors.

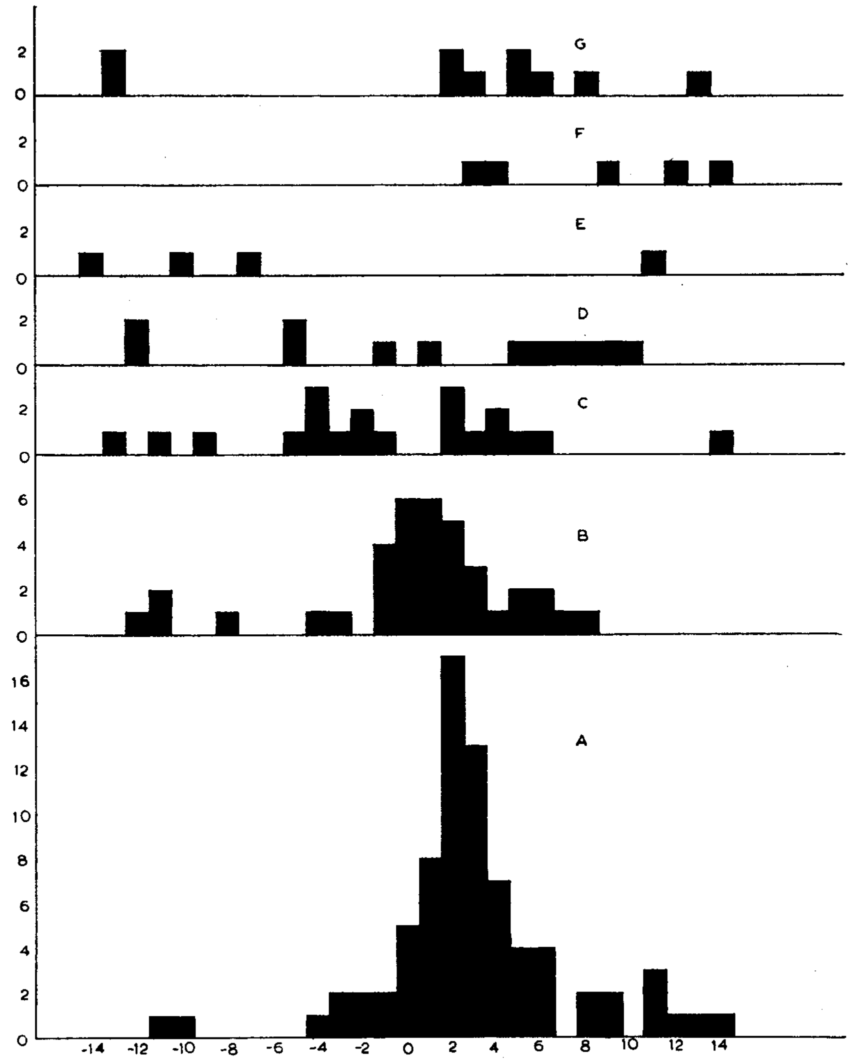

Fig. 4. — Histograms illustrating the relationships between the phase of the moon and dates on which adults of *Povilla adusta* have been observed.

Abscissa: Number of days after full moon.
Ordinate: Number of observations.

A. Lake Victoria. B. In laboratory from L. Victoria.
C. Lake Albert. D. Lake Edward.
E. Lake Tanganyika. F. Lake Kivu.
G. Other localities.

The possible light factors which might influence the larvae include the times of moonrise, zenith and moonset, and the phase of the moon itself as indicated by the light intensity. Since the first three of these factors are not firmly fixed in relation to the phase of the moon, the dates on which swarms of *Povilla* had been observed were examined to determine whether a closer relationship could be detected between them and any of these factors than they showed to the date of full moon. No closer relationship could be found, however, and it is concluded in the absence of more critical methods, that the light intensity of the moon may be the variable to which the larvae respond. It would clearly be of great value to know whether the light intensity threshold of the larva lies in the range immediately below the intensity of full moon. In any case, whatever the stimulus may be, there are two ways in which a series of stimuli might produce an emergence rhythm. Either a single stimulus might act as a trigger on those individuals which were in a receptive condition, or a series of stimuli at regular intervals might induce a rhythm in the larvae, this rhythm being translated into an emergence rhythm at maturity. The first of these hypotheses suffers from the disadvantage that it will not account for the mainenance of the rhythm despite variations in the meteorological conditions. There are, however, relatively few evenings when the moon is obscured throughout the night, Mr. D. J. BARGMAN of the Meteorological Office, Entebbe, suggesting a figure of about one night in ten. The second hypothesis suffers from the disadvantage that, although the number of days from one full moon to the next varies from twenty-nine to thirty, the peak emergence night is usually the second after full moon. There is some variation, however (see Fig. 3), and it is found that a slightly closer relationship can be demonstrated between the date of emergence and the date of full moon three months before. This difference, although insignificant, might be attributed to the induction of a rhythm early in larval life, in the same way as was found by HARKER (1953) in the diurnal rhythms of mayfly larvae.

Although conclusive results must await the development of a satisfactory method of rearing the larvae under controlled conditions, some preliminary experiments show that the normal emergence rhythm, both in relation to the diurnal and the lunar cycles, is maintained after ten days in darkness, and in the case of two individuals, after six weeks in darkness. These results lend some slight support to the hypothesis that the rhythm is induced by a succession of stimuli at regular intervals.

SPECIAL FEATURES OF THE BIOLOGY OF *POVILLA ADUSTA*

In many respects the biology of *Povilla adusta* resembles that of the widespread genus *Ephoron,* but it does possess certain features which have not been encountered in other mayflies. The most striking of these are the filter-feeding system, the production of a silk-like substance and the lunar rhythm of emergence. Only the last of these can be regarded as an adaptation to a tropical environment, for reasons which will be discussed. The other two features might occur in mayflies anywhere and reasons have been given for suspecting that *Ephoron* may feed and produce silk in the same way as *Povilla.* The habit of burrowing in wood is unusual in fresh-water animals and it is of interest to note that both VEJHABONGSE (1937) and ULMER (1939) have recorded *Povilla* larvae boring into wood and bamboo in Asia.

DISCUSSION

The most striking feature of the biology of *Povilla adusta* is its lunar rhythm of emergence. HORA (1927) suggested that certain Ephemeroptera (not *Povilla*) emerge in relation to the phase of the moon, but his evidence is slender and in at least one example is apparently based on an incorrect estimate of the date of full moon. *Povilla adusta* thus appears to be the only mayfly in which a lunar rhythm of emergence has been confirmed.

Apart from certain examples the significance of which is obscure (BROWN, BENNETT, WEBB and RALPH 1956, BROWN, SHRINER and RALPH 1956, etc.), the vast majority of known examples of lunar rhythms occur in marine organisms; this is perhaps understandable in view of the diverse effects of the tidal cycle on the littoral zone from which many of the examples come. There is, however, a small number of examples of lunar rhythms recorded in non-marine animals. RAY and CHAKRAVERTY (1934) recorded a lunar rhythm in the sexual activity of a parasitic Ciliate living on the gills of a fresh-water mussel at Calcutta; MACDONALD (1956) has recorded a lunar rhythm of emergence in the « Lake-fly » of Lake Victoria, and VANDERPLANK (1941) has recorded a lunar rhythm in the activity of *Glossina.* WILLIAMS (1936) and WILLIAMS and SINGH (1951) suggested that moonlight influenced the flight of certain nocturnal insects, but this appears to be an artefact (WILLIAMS, SINGH and EL ZIADY 1957).

Before considering the significance of the lunar rhythm of *Povilla,* it will be convenient to mention the significance of sexual rhythms in general. The possession of a sexual rhythm may be of adaptive value in two ways. Firstly, in any environment the population density of the sexual phase will periodically be raised to a level which could otherwise only be attained by an increase in total population density. This will presumably have the effect of increasing the chances of sexual union. Secondly, in a fluctuating environment, the rhythm may ensure that the various stages of the life-history are present only when the environment is most suitable for them. The accuracy with which the sexual phases of different individuals are synchronised clearly varies widely from species to species. Close synchronisation may be of especial significance to species of three kinds — those which can only maintain a low total population density, those in which there is a high mortality rate before sexual development and those in which the sexual phase is brief. Such close synchronisation might be obtained through a response to more than one environmental cycle and a striking example of this is provided by the Pacific palolo worm *Eunice viridis* (GRAY), the swarms of which appear in relation to a conjunction of seasonal, lunar and diurnal factors. In most of the animals which have been studied, however, such close synchronisation is not observed, the sexual cycles being related only to seasonal factors. In temperate regions, daylength changes have been found to be of great importance in regulating gonad development in certain vertebrates (ROWAN 1926, 1938, BISSONNETTE 1931 and others), while in the small number of tropical animals which have been studied, seasonal changes in rainfall seem to be significant (WAIT 1931, WALOFF 1946, CHAPIN 1956). In all of the environments occupied by these examples, seasonal changes are marked and have profound effects on the lives of the animals.

The tropical lake is an example of an environment in which seasonal changes are greatly reduced. In most tropical environments, the seasons are marked by primary and secondary effects of the rainfall changes. The tropical lake, however, is not greatly influenced by these changes, although there are doubtless small changes in turbidity and salinity. The two most important factors, temperature and oxygen concentration, are remarkably constant throughout the year. Fish (in the press) found an annual temperature range of only 2° C. at a locality in the northern end of Lake Victoria, while TALLING (1956) working at the same spot, found, over a period of one week measured at hourly intervals, that the oxygen concentration varied between 6.7 and 7.4 mgm l., corresponding to a range from 80 % to 90 % saturation at 24° C. MARLIER (1956) has also commented on the extreme constancy of conditions in tropical lakes. In view of this constancy, it is to be expected that certain species living in tropical lakes would breed continuously throughout the year and this is in fact observed. LOWE (1956) found that samples of the fish *Tilapia esculenta* collected in Lake Victoria at all times of the year always contained some breeding individuals, although the proportion rose during the wettest season and fell during the driest season of the year. Other species, however, may be expected to display various degrees of synchronisation of the sexual phase, and unless they are able to respond to the small seasonal changes, must rely on the two environmental cycles which remain, the diurnal and lunar cycles. It is therefore of interest to note that two examples are now known of animals living in Lake Victoria which possess lunar rhythms. One of these is *Povilla,* in which the rhythm operates in conjunction with a diurnal rhythm. The other is the « Lake-fly » studied by MACDONALD (1956). Lake-fly is a general term including a mixture of species of Chironomid and Chaoborid which periodically appear in vast mixed swarms. MACDONALD found that the great majority of these swarms are seen during the fortnight following the new moon; he makes no mention of any diurnal rhythm of emergence but this would be difficult to detect from records of swarms seen, since the adults live at least twelve hours and possibly longer.

There are thus three examples known of animals living in Lake Victoria which display sexual rhythms. In *Tilapia* there is a feebly marked seasonal rhythm; in Lake-fly there is a moderately marked lunar rhythm, possibly associated with a diurnal rhythm, while in *Povilla* there is a very marked lunar and diurnal rhythm. It is tempting to try to relate the apparent difference between the accuracy of synchronisation in Lake-fly and *Povilla* to differences in their life-histories. In Lake-fly the sexual stage probably lasts at least 1/120th. of the total life, while in *Povilla* this fraction is only 1/2000th. of the total life. Neglecting other factors, therefore, *Povilla* would clearly require far more accurate synchronisation to obtain an equivalent adult population density. There are, however, many other factors which might also account for the difference.

From this account it may be concluded that the lunar rhythm of *Povilla adusta,* and perhaps those of other organisms, is an adaptation to an environment in which seasonal effects are reduced. Lunar rhythms might therefore be expected to occur more frequently in animals living in such environments. The reduction of seasonal effects may be more likely in tropical aquatic environments than elsewhere and it is therefore of interest to note that, of the 94 species possessing lunar rhythms listed in CASPERS (1951), about 10 % live in aquatic habitats within

10 degrees latitude of the Equator. This figure is considerable when it is borne in mind that zoologists are rare in the tropics compared with Europe and North America, the other two regions from which numerous examples of lunar rhythms are known.

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SUMMARY

1. Previous observations on *Povilla adusta* are briefly mentioned.
2. The biology of *P. adusta* has been studied at Kaazi which is on the north coast of Lake Victoria.
3. The eggs are laid in masses each containing between 1000 and 2500 eggs. They are believed to hatch in the field after eleven or twelve days.
4. The larvae burrow in wood and other plant materials by means of the mandibular tusks. The burrows are lined with a silk-like material which is produced by the Malpighian tubules.
5. The larvae feed by filtering water through brushes of pinnate setae borne on the tusks and forelegs.
6. The possibility that the larvae of other Polymitarcidae feed and produce si k in the same way as *Povilla* is discussed.
7. The larvae remain in their burrows throughout the day but swim for at least part of the night, even after two weeks in constant darkness.
8. Various unsuccessful methods of determining the duration of larval life are described; the results of rearing larvae in cages in the lake support Corbet's estimate of three or four months.
9. The adults display a marked diurnal rhythm of emergence and are usually seen only between 7.30 and 9.p.m. The adult life is only about one and a half hours.
10. In Lake Victoria, but not in the other lakes studied, the adults also display a marked lunar rhythm of emergence, the greatest number emerging on the second evening after full moon.
11. The possible means by which this rhythm is induced are discussed. It is concluded that variations in the light intensity of the moon may induce a lunar rhythm in the larvae.
12. The specialisations observed in the biology of *Povilla adusta* are discussed in relation to the biology of other mayflies.
13. The significance of sexual rhythms in animals is discussed.
14. The lunar rhythm of *Povilla adusta* is considered to be an adaptation to an environment in which seasonal fluctuations are reduced; it is suggested that other examples of lunar rhythms may be adaptations of a similar kind.

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