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Introduction

The species of the order *Ephemeroptera* are larvo-aquatic; the larvae being especially well adapted to an aquatic life. The adults of *Ephemeroptera* emerge as sub-imagines, which — in most cases — moult to yield the imagines. The mayflies are the only insects that undergo an ecdysis after having acquired functional wings (IMMS, 1948). In some species the adults do not moult, but complete the life as sub-imagines; in some only the male sub-imago moults, and some show a partial exuviation in that the imago retains the sub-imaginal skin of the wings (EDMUNDS, 1956).

The adults of *Ephemeroptera* do not feed (VERRIER, 1956). SPIETH (1940) considers that the adult males of many species imbibe water; his evidence for this assumption is vague, and his assumption is not generally accepted. NIELSEN (1950) states that the mayflies do not imbibe water as adults. They are thus unable to replenish the water lost through evaporation.

RÉAUMUR (1742) observes, giving no reference as to species (cf. SHARP, 1901), that the mayflies emerge in the evening and that most live for a night or less. RÉAUMUR'S (1742) observations on emergence and longevity are not acceptable as a general statement for the whole order. The longevity of adult mayflies has been shown to vary with the species; some species live for about an hour (GILLIES, 1954; HARTLAND-ROWE, 1958) others survive for days or weeks (CRASS, 1947). The longevity of a species of mayfly (adult) varies also with the climatic conditions. A low temperature and a humid atmosphere would decrease the evaporation and thus prolong the life of the adult *Ephemeroptera*. Emergence is not restricted to the evening (VERRIER, 1956); indeed CRASS (1947) found that most of the species studied by him in Natal and the Eastern Cape emerged during the day.

After emergence some species show a sub-imaginal flight activity before settling down to moult; the subsequent flight of the imago is a mating flight. Mention must be made of the fact that a few species moult in flight (HARTLAND-ROWE, 1958; EDMUNDS, 1951, 1956), and that parthenogenesis occurs in *Ephemeroptera* (VERRIER, 1956; DEGRANGE, 1954). The times of flight activity vary within the order. VERRIER (1956) writes (*loc.cit.:* pp. 45—46): "On attribue généralement une activité crépusculaire ou nocturne aux Éphémères. Ils constituent, en effet, une partie importante de la faune ailée qui évolue autour des sources de lumière intense (lampadaires, phares d'automobile) les soirs des chaudes journées d'eté; car ces Insectes, comme beaucoup d'animaux nocturnes, manifestent un phototropisme positif très net. Cependant les observations abondent, relatives à des vols d'Éphémères à toutes les heures du jour.".

EATON (1883) points out that the duration of the imaginal stage is related to the time the same species has spent as a sub-imago. Thus a species that spends only a few minutes as a sub-imago has a shorter life expectancy as an imago than has a species that spends twenty-four hours as a sub-imago (EATON, 1883). This relation has been confirmed by several workers. It should be mentioned, however, that CLEMENS (1917) and LYMAN (1944a) have drawn attention to the effect of temperature on the duration of the sub-imaginal stage; as expected, they found that exuviation took place earlier at a high temperature than it did at a low temperature.

Our concept of the biology of the adult mayflies is in the main based on studies that have been carried out in the temperate regions. The reader is referred to VERRIER'S (1956) book on the biology of mayflies.

The literature that exists on tropical *Ephemeroptera* is almost exclusively taxonomic; studies on the biology of tropical mayflies appear to be few. And our knowledge of the biology of the adult stages of tropical mayflies is very limited. GILLIES (1954) and HARTLAND-ROWE (1955, 1958) have made valuable contributions in the latter respect. GILLIES (1954) observes that adults of *Prosopistoma africanum* GILLIES can only be found during the forty-five minutes immediately following daybreak, and considers it probable that this species emerges at dawn. It is likely that the adult life of *Prosopistoma africanum* is short; lasting from dawn till forty-five minutes after daybreak (GILLIES, 1954). HARTLAND-ROWE, working on *Povilla adusta* NAVÁS, finds that this species shows a lunar periodicity of emergence in Lake Victoria. The latter species emerges after sunset, and flies between 1930 and 2100 hrs. (East African Standard Time), surviving for about an hour only (HARTLAND-ROWE, 1958). Thus the adults of the two species that have been studied in detail in East Africa, have in common a very short life, but they differ with regard to the times of emergence and flight activity. Notes on the biology of the adult stages of tropical mayflies are scattered in the taxonomic literature (HARTLAND-ROWE, 1958), but they contribute little to our knowledge. The mayflies described and listed in the taxonomic papers have often been collected at light at night (cf. BUXTON, 1937; NEEDHAM & MURPHY, 1924; TRAVER, 1956; GILLIES, 1957a; HORA, 1927; ULMER, 1924, 1930; KIMMINS, 1948, 1955, 1956), but this tells us little apart from the fact that a nocturnal flight activity seems common in the tropical mayflies. (In the present communication the word "nocturnal" has been used in its widest sense to cover activity taking place between sunset and sunrise.) Observations on nocturnal swarming of tropical mayflies found in literature dealing with other orders of insects are suggestive, but as the species of *Ephemeroptera* to which the information relates have not been identified, such observations are not very helpful. RAO & RUSSELL (1938) working on mosquitoes in India, observed mayflies swarming at daybreak. CORBET & TJØNNELAND (1955) working on *Trichoptera* in Uganda, considered the group activity of nocturnal mayflies (*Povilla adusta* excepted) to be bimodal.

It is my hope that the present communication will increase our knowledge of certain aspects of the biology of the adult mayflies in the tropics. The adults of *Ephemeroptera* are, as we have seen, vulnerable insects, especially so in certain tropical climates. The flight activity of mayflies is a very important aspect of their biology, and one would expect the times of activity to be adjusted — in one way or another — to the environmental conditions so as to make it possible for the tropical mayflies to complete their reproduction, the most important aim of the adult life. In this particular case, one would expect them to be nocturnal in their flight activity habits. Although a few species have been noticed to swarm in bright sunlight at Jinja, Uganda, where the present study was carried out, these species form a negligible part of the mayfly fauna found at Jinja, both in number of species and in the number of individuals. The rest of that fauna is either exclusively or predominantly nocturnal as far as the flight activity is concerned. The assumption made above is therefore confirmed, but several questions remain. What nocturnal flight activity patterns have been formed in tropical mayflies? Are the flight activity patterns of a plastic type, allowing the species to take advantage of any suitable climatic period that occurs during the night, or is the pattern a rhythmic one? If the patterns are of a rhythmic type, questions arise as to what factor (or factors) is likely to determine these rhythms. The latter question cannot be fully answered from a field study alone, as mentioned by HARKER (1958). The next question concerns the influence of the different external factors on the population, its flight activity pattern as well as on the flight activity itself. If patterns other than strictly unimodal ones occur, what is then the distribution of individuals belonging to different age groups and — if different emergence populations overlap — how are such groups distributed within the different activity peaks? The last question leads on to another important one. What is the total flight activity of one single emergence group? Do any species have to survive a tropical day (or more) in order to complete their adult life cycle? Lastly there remain questions about lunar cycles of emergence and any seasonal effects on the flight activity patterns or the size of the population. The question regarding lunar periodicities of emergence in certain mayflies at Jinja was studied by CORBET (1958c) in 1956. Running a Robinson mercury vapour light trap for a hundred consecutive nights, CORBET (1958c) found that *Povilla adusta* was the only species of *Ephemeroptera* studied that showed a lunar periodicity of emergence in Lake Victoria. The species dealt with in the present paper, are the same as were chosen by CORBET (1958c) for his study on lunar periodicity of emergence. I have also employed the same type of light trap. CORBET (1958c) did not study the flight activity of the species of *Ephemeroptera* and he did not separate the sub-imagines from the imagines in his records. The present study is accordingly somewhat more detailed than CORBET'S (1958c); it also covers a longer period of time. It provides therefore a valuable check on the simplified method of approach employed by CORBET (1958c) and may accordingly be of interest in future research in this line.

The present study should have some practical importance. It is well known that the larvae (and to a certain extent also the adults) of mayflies are important as food for fish. The present study, although limited in its scope, may therefore be of interest to the scientists engaged in fisheries research on the lakes of East Africa. Furthermore, the adults of *Ephemeroptera,* together with adults of other larvo-aquatic insects (*Trichoptera, Chaoborus* spp. (*Diptera*) and *Chironomidae* (*Diptera*)), have a certain nuisance value at or near the shores of Lake Victoria and the Victoria Nile. This applies particularly to the nocturnal and phototropic insects, as mentioned by BERTLIN & OLIVIER (1954), CORBET (1958a) and CORBET & TJØNNELAND (1955). Thus, BERTLIN & OLIVIER (1954) report from the building of the Owen Falls Dam (*loc.cit.* p. 673): "Throughout the contract period, nuisance was caused by heavy swarms of Lake (May) fly, which are attracted by lights. Although these insects did not bite they were a nuisance to workmen, foul fishy-smelling messes were left under lamp posts where swarms had died, and their remains on painted surfaces (except cellulose paints) proved corrosive in the long run.". With increased industrialisation around the lake the insect nuisance will probably become more generally felt. A knowledge of the flight activity of the most abundant and troublesome species should therefore prove of value, as mentioned by Corbet & Tjønneland (1955).

No attempt will be made to review the extensive literature that exists concerning diel activity in insects. Reference is made to Harker (1958) who has recently written a survey of the diel rhythms in the animal kingdom. Harker (1958) being mainly concerned with the true nature of the various rhythms found, has stressed the work done under controlled conditions in the laboratory. She is less concerned with the activity as expressed by populations in nature, but some of the methods employed and some of the results achieved in field studies of insects, are briefly mentioned. Haddow (1954) has reviewed literature concerning the biting activity of mosquitoes.

In studying the flight activity of nocturnal and phototropic insects in the field, light traps have often been used to attract and collect flying insects. This method has met with some criticism (cf. Harker, 1958). There can be no doubt, however, that information gained by using light traps — provided that the information is critically applied — can substantially augment our knowledge of the flight activity of nocturnal insects, as claimed by Park (1940) and as demonstrated by Williams (1935, 1936, 1939, 1940, 1951), Williams, French & Hosni (1955), Williams, Singh & El Ziady (1956), Brown (1954), Sylvén (1958) and others. It is my hope that the present communication will help to confirm the view that light traps can be of great value in studying the activity of nocturnal insects, and that the results presented may also prove of interest to workers engaged in field activity studies of species belonging to other orders of insects.

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Procedure

Jinja (Busoga Province, Uganda) is situated at the point where the Victoria Nile leaves Lake Victoria (Fig. 1). As Jinja (latitude: 0° 25.5′ N.) is practically on the equator, the length of the day is approximately the same as the length of the night; and the length of the night varies by a couple of minutes only throughout the year.

A Robinson mercury vapour light trap (design no. 862769; ROBINSON, 1952) fitted with a 125-watt mercury vapour bulb, was used to attract the adult mayflies. The use of light traps in studying the flight activities of nocturnal phototropic insects is based on the assumption that the number of individuals of a species caught by a light trap during successive fractional sampling periods throughout the night is an approximate measure of the flight activity of the same species during the same periods of that particular night (CORBET & TJØNNELAND, 1955). Further implications are mentioned by CORBET & TJØNNELAND (1955).

The use of light traps imposes restrictions on the interpretation of the data collected. It is unlikely that the distance from which the trap is able to attract the insects is the same for all the species concerned. And all species may not be equally attracted by the light emitted by the mercury vapour bulb. Were it only for the two reasons mentioned, it would be fallacious to base a conclusion as to the relative abundance of the different species in nature on the relative catches of the same species in a light trap. Nor should one feel too confident about the sex ratio, as expressed by the catches in the trap, of a species. The possibility cannot be ignored that one sex is more strongly attracted to the trap than the other. Until more is known of the phototropic responses in *Ephemeroptera*, it seems safe to assume that the two sexes are not equally attracted, as the eyes of the males differ considerably from those of the females (cf. NEEDHAM, TRAVER & HSU, 1935). It is furthermore possible that the sub-imagines and imagines of each sex show a somewhat different response to the same source of light. In the present paper I have accordingly decided to treat the sub-imagines and the imagines of each sex and species as separate groups. The question arises: Is it possible that the phototropic response of any of these groups changes during their period of activity? EDMUNDS, NIELSEN & LARSEN (1956) working on *Ephoron album* (SAY) found that the females were not positively phototropic immediately prior to — and during — copulation; but exhibited a pronounced positive phototropic reaction a few minutes after the copulation had taken place. To a less extent, a similar variation in the phototropic response was also evident in the male. As copulation is usually accomplished in a very short time in *Ephemeroptera* (EATON, 1883; DESPAX, 1949), the variation in phototropic response reported by EDMUNDS, NIELSEN & LARSEN (1956) is not likely to be of any great importance in a flight activity study, but it should nevertheless be borne in mind.

Another complication that is experienced when interpreting flight activity data gained by using light traps, is that it is not possible to relate accurately population density and flight activity with the light trap catches. Thus the same numeric catch may result from a) a large population being to a great extent prevented from flying; b) a large population on the wing, but prevented from entering the trap due to an unfavourable external factor (a strong wind); or c) a small population, on the wing and flying under conditions that make it easy for the individuals to enter the light trap (no wind). It follows from what has been mentioned above that a study of the flight activity of nocturnal insects by means of light traps, is more a study of consistency of tendencies apparent from the samples taken, than a study of the actual number of insects caught by the trap.

A permanent site was found for the Robinson mercury vapour light trap between the E.A.F.R.O. laboratory and the lake shore. The distance from the laboratory building to the trap was ten metres; the distance from the trap to the nearest part of the lake shore was about 150 metres (horizontal projection), the vertical distance between the trap and the lake level was about thirty-five metres. The site of the trap is identical with that mentioned by CORBET & TJØNNELAND (1955); the distance of the trap from the lake shore given by these authors is exaggerated. In the present study, the trap was placed so that the distance from the mercury vapour bulb to the ground was about one metre. This arrangement reduced the intensity of illumination on the ground and caused fewer insects to be flight inhibited in the vicinity of the light trap.

From the site of the trap one had a view of most of the Napoleon Gulf. The view towards the south-east (Nassau Point and beyond) was only a little obstructed by a few trees. Towards the south, the view was considerable obstructed by trees growing near the site of the trap; and towards the south-west the view was somewhat obstructed by trees and by rising ground. No parts of the outlet of the Victoria Nile — or the Victoria Nile itself — can be seen from the site of the light trap. Behind the laboratory, towards the north, the ground rises very gently towards the heavily built up parts of Jinja Township. The trap was shaded from these parts by the laboratory as well as by groups of trees.

The trap was always run without any protective cover for the bulb, and trapping was not discontinued during rain.

From the 14th September 1956 till the 6th September 1957 (referred to as year I in the present paper) the trap was run every seventh night. The resulting fifty-two sampling nights are listed by TJØNNELAND (1958b). Throughout the nine synodic months from 7th October 1957 till 29th June 1958, referred to as year II, the trap was run every night. When employed for these whole night catches in year I and year II, the bulb was switched on at 1815 hrs. (East African Standard Time); *i. e.* twenty to fifty minutes before sunset depending on the time of the year. The mercury vapour bulb attains its full brilliance three to four minutes after having been switched on. Full brilliance was therefore achieved before the trapping started at sunset. By starting the trapping at sunset, the data relate to a time system based on sunset and sunrise, a system recommended by LUMSDEN (1952) for this type of research.

In year I, the contents of the trap were emptied every ten minutes throughout the sampling nights. Thus each sampling night — with two exceptions — yielded seventy-two ten minute samples. The exceptions were caused by a cut in the power supply that lasted for one hour in one sampling night, and lasted for half an hour on another occasion. Working with ten minute sampling periods, it is essential to cut the time involved in emptying the trap. Adopting the methods used and described by CORBET & TJØNNELAND (1955), the time lost in emptying the trap can be reduced to eight to ten seconds.

In year II, the trap was only emptied twice every night. The trap was first emptied one hour after sunset, then left to run itself until sunrise, when it was emptied for the second time. The trap arrangement used by CORBET & TJØNNELAND (1955) was slightly altered. Instead of using a glass receptacle, containing a ninety per cent solution of alcohol, in the trap; I employed a cylindrical metal receptacle divided in four equal chambers by vertical partitions (Fig. 3) and containing a fifty per cent solution of alcohol. The cardboard sleeves, used in year I, were exchanged for sleeves made of wire gauze. This was done to prevent heavy rainstorms from filling (or dissolving) the sleeve and causing a short circuit when the trap was left unattended during most of the night.

For each ten minute sampling period in year I, records were kept of the approximate temperature, the relative humidity, wind direction and wind strength near the site of the light trap. The temperature and humidity records were taken from the thermohygrograph chart for the night in question. The temperatures were recorded to the nearest degree centigrade, the humidity was recorded to the nearest five or ten per cent of relative humidity. The thermohygrograph was placed thirteen metres from the laboratory, at a distance of eight and a half metres from the light trap. The thermohygrograph stood on a stool, sixty-four centimetres high, and was sheltered from the rain by a metal roof. The roof was made in two sections, one above the other, so that air could pass between them. The temperature and the humidity of any ten minute sampling period was regarded as being that of the beginning of the period. The direction of the wind experienced at trap level in any period, was likewise regarded as being that of the beginning of the same period. The wind direction was recorded as indicated by a very sensitive wind vane, the dial of which was divided into segments, and given a permanent orientation with regard to the lake shore (Fig. 2). The wind vane stood on a table, ten metres from the laboratory, three metres from the trap and ninety-five centimetres above the ground. An anemometer of a "counting" type registered the amount of wind — in units of ten metres — experienced at a height of 1.65 metre above the ground. The anemometer was placed twelve metres from the laboratory, and seven and a half metres from the light trap. The amount of wind was of course recorded at the end of the ten minute period. The intensity of rain, the amount of clear sky and the extent to which the moon was covered by clouds in any of the ten minute sampling periods of year I, was recorded according to visual observation; the intensity of rain being recorded at the end of the period, the other two factors being recorded at the beginning of the period. A lightmeter (a Multiflex Luxmeter type III with a photocell type S 145) was read in the middle of each ten minute sampling period. The photo cell of the lightmeter had to be placed behind the laboratory, so that the sensitive cells were not affected by the light from the mercury vapour bulb nor by the lights of the street-lamps north of the laboratory buildings. The arrangement was far from being ideal, as the photo cell of the lightmeter was not fully exposed, and when the moon was low, the shadow of the building fell on the photo cell. Otherwise some of the information gained by using the lightmeter was indicative and of value.

During year II, records were kept of temperatures and humidities (at midday — by midday is meant the real midday, half way between sunrise and sunset — at sunset and at sunrise), amount of wind and the amount of precipitation (observation periods: sunrise till midday; midday till sunset; sunset till one hour after sunset; from one hour after sunset till sunrise). The temperature and the humidity were recorded by means of whirling psychrometers, and measured in the open shade. The thermohygrograph recorded the temperature and humidity during the night to supply information on the variations of these two climatic factors between sunset and sunrise.

The meteorological observations recorded by me are affected by the proximity of the laboratory buildings and because the recording instruments were close to ground level; this is particularly true for the observations on wind direction and wind strength. The temperatures and the humidities as recorded by the thermohygrograph in year I and year II, are not quite exact. The thermohygrograph was not enclosed in a meteorological hut, and condensation, particularly in the morning, influenced the temperature and the humidity recordings. Thermohygrographs are also somewhat slow in registering changes in temperatures and humidities. The temperatures as registered by the thermohygrograph in year I and year II are a little too low. The difference between the temperatures registered by the thermohygrograph and the control thermometers, was never found to amount to more than a degree centigrade, and it was usually much less. The temperatures and humidities as registered by the whirling psychrometers in year II, provide more reliable information.

Of the thirteen species chosen for the present study, two were abandoned: *Procloëon cylindroculum* KIMMINS because it was too easily confused with some undescribed species; *Ephemera aequatorialis* KIMMINS only yielded three specimens in two years and was abandoned for this reason. The remaining eleven species are listed below.

Family *Baëtidae:*

Centroptilum corbeti KIMMINS, *Centroptilum notabile* KIMMINS, *Cloëon dentatum* KIMMINS.

Family *Heptageniidae:*
Afronurus ugandanus KIMMINS.

Family *Leptophlebiidae:*
Adenophlebiodes decoratus KIMMINS[1], *Euthraulus bugandensis* KIMMINS, *Euthraulus curtus* KIMMINS, *Hagenulus fasciatus* KIMMINS.

Family *Polymitarcidae:*
Povilla adusta NAVÁS.

Family *Tricorythidae:*
Tricorythus maculatus KIMMINS, *Tricorythus tinctus* KIMMINS.

P. adusta was described in 1912 (NAVÁS, 1912) and has a wide distribution in Africa (cf. NAVÁS, 1930; VERRIER, 1951; HARTLAND-ROWE, 1958; and KIMMINS, 1948). *T. maculatus* was described in 1948 (KIMMINS, 1948) and the other nine species were described by KIMMINS in 1956 (KIMMINS, 1956). In the following species, sub-imagines and imagines have been recorded separately for both males and females: *C. corbeti*, *A. ugandanus*, *A. decoratus*, *E. bugandensis*, *E. curtus* and *T. maculatus*. *H. fasciatus* was only found as imagines in my light trap. The males of *T. tinctus* that came to the trap were all imagines; the females of *T. tinctus* were all sub-imagines. Indeed, it is unlikely that the females of *T. tinctus* moult at all as adults (vide infra). For *P. adusta* the sub-imagines and imagines have been pooled for both males and females. For the remaining two species, I was not able to record more than the imagines of *C. notabile;* nor was I able to record more than the male imagines of *C. dentatum*. *C. dentatum* has also been found to fly after dawn. and was dropped altogether in year II. The females of *E. bugandensis* and *E. curtus* caught during the first seven sampling nights in year I were not identified.

The treatment of the catch in year I was identical with that employed and described by CORBET & TJØNNELAND (1955). In order to be able to cope with the work involved in sorting and identifying the catch in year II, a method for sub-sampling the catch was found whereby the work (as well as the number of insects dealt with) was reduced by a half. The receptacles used in year II have already been described. A receptacle, when in the trap, was given a fixed orientation with regard to the lake shore (Fig. 3). The mayflies on arrival in the light trap distributed themselves in the four chambers of the receptacle, and it was discovered that the *Ephemeroptera* from two diagonal opposite chambers yielded approximately half the total catch. Appendix 1 (p. 63) gives

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[1] The name of the species is preoccupied, and Mr. D. E. KIMMINS (personal communication) has informed me that he will re-name this species.

details on the number of various species of mayflies found in the two lots of chambers: (1 + 3) & (2 + 4), after the trap had been run for various intervals on six different evenings in 1957. The chi-square values are nearly all below 3.841, and support the theory that the mayflies were evenly distributed between the two lots of chambers. As will be seen from Appendix 1, the method of subsampling is less reliable when the total number of individuals caught is low; but the method gives a good idea of the fluctuations in the catches from night to night, the subject of prime interest in this connection. On occasions in year II, very heavy catches of *C. notabile* were experienced, and the number of *C. notabile* had to be estimated. This was done by spreading out the sample from the two chambers in a tray, using a counting frame. As mentioned (TJØNNELAND, 1958a), the error in this process cannot be satisfactorily estimated. A knowledge of the exact number of *C. notabile* caught on these peak nights is, however, of less importance.

In analysing and presenting the flight activity data of the different species, the activity is conveniently expressed in terms of WILLIAMS' (1935) modified geometric mean values (gmw) against the time of night. The gmw-values stress the consistency of results, and WILLIAMS' method has accordingly been extensively used in the present study. In estimating the flight activity data, I have not allowed for the fact that the trapping was started three minutes too late on the evening of the 15th February 1957; a fact that was not discovered until the following morning. Nor have I allowed for the fact that the bulb of the light trap had to be changed on a few occasions when the trap was running in year I. This happened very rarely and only took less than a minute to do.

It is important to know to what extent the times of the different activity peaks shown by a species varies when the different sampling nights in year I are compared with each other. The flight activity histograms, referred to in the previous paragraph, supply little information on this point. I have therefore prepared peak frequency histograms for all species. The peak frequency histograms have been worked out in the following manner. For every single sampling night in year I, the highest number of mayflies of the same stage, sex and species (exception: *P. adusta*, cf. p. 13) caught in any ten minute sample, has been regarded as being the activity peak for that particular night and listed — as one event — against the ten minute sampling period in which it occurred. If a bimodal activity was apparent, the highest number caught in any ten minute sampling period before midnight was counted as one event, and the highest number caught in any ten minute sampling period after midnight was counted as another. Ultimately the number of events has been summed up for all the sampling nights and listed against the ten minute sampling period in which they occurred. The method employed in making these histograms, is not without faults. The method thus does not guard against the effects aberrant climatic conditions have on the numeric size of the catch. Highly unfavourable meteorological conditions persisting throughout the times when the species group has its activity maxima, will suppress the catches. If the severe conditions subside after the normal activity peak is over, the number of insects caught may increase and surpass the number caught during any ten minute period within the normal activity peak. The resulting aberrant peak catch will then be counted as one event in the peak frequency histogram.

The gmw-values have also been used in expressing some of the wind strength data. And WILLIAMS' (1935) method has also been employed in analysing data concerning lunar periodicities of emergence. In the latter case, the number of insects (gmw-values) have been plotted against the age of the moon (in whole days from the previous new moon) at 0000 hrs. GMT of the various sampling nights during the nine synodic months in year II. The moon ages have been taken from "The Nautical Almanac and Astronomical Ephemeris" for the years 1957 and 1958. The gmw-values have here been based on the arithmetic number of insects found in two of the chambers in each of two receptacles employed.

Diagrams showing the night to night fluctuations in the catches of the different species have been prepared. The number of insects is here expressed as log (n + 1) against the night when the catch was taken. The number n here stands for the arithmetic number of insects found in the two chambers of the two receptacles employed, that is approximately half the total catch. The use of logarithms in this connection may be objected to, as they tend to emphasize the smaller, and more unreliable, numbers than the higher ones. But, in order to express the catches graphically, it was necessary to employ the logarithms of (n + 1).

As a consequence of what has been said earlier, statistical treatment of the data has been avoided. Such treatment would be very complex, and as long as the size of the populations and the size of the emergence groups are not known, there can be considerable doubt regarding the value of a statistical treatment of the data.

In order to gain some knowledge of the longevity of the adults of various species of mayflies as well as of the time of moulting, individuals were collected when they came to light in the evening and isolated singly in small plastic boxes. The boxes were usually kept indoors; and the lid of the boxes were only partially closed, leaving a slit in the top of the box. The slit made it possible for the air to circulate freely, but made it impossible for the insect to escape. The boxes were inspected at irregular intervals and the number of insects alive were noted, and, when sub-imagines had been isolated, the number of insects that had moulted were recorded. Some of the results are presented in Appendix 2 (p. 63). It should be realized that the temperature and the humidity in the laboratory, where the boxes were kept, varied less over the twenty-four hours, than they did in the open. The night temperature in the laboratory was generally somewhat higher than the night temperature outside the laboratory. During the day, the temperature in the open was the higher. As expected, the humidity at night was higher in the open, whereas the higher humidity during the day was generally experienced in the laboratory. It is likely therefore that the moulting takes place somewhat earlier when the sub-imagines are kept in the laboratory. Insects that can survive a tropical day (or more) in nature would have a longer life expectancy in the laboratory, where they are not subjected to the relatively dry air in the open. But it must be added that we do as yet know little about the humidity experienced in the places where the mayflies spend the day resting at Jinja.

It seems possible from the flight activity histograms to form an idea of the time of emergence of the various species. This was confirmed by studies in the field.

It was not possible to keep all the identified *Ephemeroptera* collected during the present study, but small representative collections have been kept. One of these collections has been deposited in the E.A.F.R.O. laboratory at Jinja. Another collection has been left with the Zoological Museum, University of Bergen, Norway.

Remarks on some environmental factors

East Africa has been divided into several climatic zones, and Jinja is situated in the Northern Lake Victoria zone (zone 5) (GRIFFITHS, 1958). GRIFFITHS (1958) gives the following information on the climate in this zone (*loc. cit.* p. 182): "Rainfall occurs in two periods, March to June and October to November, and there is no really dry month. The annual fall is between 45 in. and 60 in., except to the south-east of Entebbe, — — —". He states further that rain falls on about 125 to 155 days of the year, and that, thanks to the proximity of Lake Victoria, the variation in mean monthly temperature is only about four degrees Fahrenheit. The relative humidity decreases from Entebbe (seventy-seven per cent) to Kisumu (sixty-two per cent); and the land and the lake breezes mainly control the direction of the wind (GRIFFITHS, 1958).

In Table I, I have listed the amount of rain for every single month from September 1954 to August 1958, as recorded by the E.A.F.R.O.

Local showers are common in the Jinja district, resulting at times in considerable differences in the amount of daily, or weekly, rainfall experienced

Table I. *Monthly rainfall in inches.*

Month	Year				Monthly sum
	1954–55	1955–56	1956–57	1957–58	
September	1.14	3.37	1.65	0.25	6.41
October	2.43	3.34	3.37	2.55	11.69
November	2.80	1.17	4.96	4.25	13.18
December	5.07	7.21	4.13	2.83	19.24
January	2.04	3.90	6.17	2.22	14.33
February	2.45	1.48	2.20	2.51	8.64
March	3.34	3.83	4.12	5.69	16.98
April	7.48	12.05	7.85	8.34	35.72
May	5.20	5.92	6.15	4.91	22.18
June	0.79	2.12	1.87	4.15	8.93
July	33.3	1.95	0.92	1.64	7.84
August	2.00	5.36	2.39	2.93	12.68
Yearly sum	38.07	51.70	45.78	42.27	177.82

even within Jinja Township. Thus, although the E.A.F.R.O. laboratory and the airport of Jinja are only a few miles apart (Fig. 1), the weekly rainfall records from these two localities usually differ. Though there is no really dry month in Jinja (Fig. 6a & 6b; Table I), and despite the fact that local showers are common, it is still possible to distinguish between rainy and dry seasons — the only seasons experienced.

Most of the rain appears to fall between sunset and sunrise. This is also evident from the rainfall figures for year II as shown in Fig. 7a & 7b. In these diagrams the amount of rainfall in inches is shown as vertical thick lines against the date and the time when the rainfall occurred. In the present publication the twenty-four hour cycle is regarded as commencing immediately after sunrise, and the date shown is that of the beginning of the cycle. During the nights, the rain is mainly experienced during the last four or five hours. This is well known, and it is further borne out by the data collected in year I. These data are presented in Fig. 4. In this figure the numbers of rainy ten minute sampling periods are shown against the time of the night when they occurred.

In Fig. 6a & 6b, the temperatures and the humidities measured at midday (dashed lines), at sunset (lines) and at sunrise the following morning (dotted lines) are shown for the 266 days in year II.

The hottest part of the year in Jinja is in January—March, just before the "long rains" start. The rainy seasons are characterized by a lower day temperature and a higher day humidity. The evenings during the rainy seasons are cool, but the cloudy nights reduce the amount of heat lost by radiation, and the really cold mornings are rare. The months immediately following the "long rains": June—July — although rather dry — are reputed to be the coldest months of the year. Otherwise the dry seasons, and especially the time between the "short rains" (October—November) and the "long rains" are characterized by high day temperatures and low day humidities. The evenings are comparatively warm; but the drop in temperature during cloudless nights can be considerable and produce some cold mornings. Such is the general pattern. But, as Jinja has not got the typical dry and wet seasons found in the northern parts of Uganda, days and nights that form exceptions to the rule, are not uncommon, as gathered from Fig. 6a & 6b. Also the onset of the rainy seasons varies a great deal from year to year, as will be gathered from Table I.

The mean temperature and the mean humidity of the different ten minute sampling periods over the fifty-two sampling nights in year I are shown in Fig. 4. As expected the fall of the mean temperature and the increase of the mean relative humidity are most noticeable during first two hours of the night. The standard deviations s(t) and s(rH) are given in the same figure.

The sampling nights in year I were generally colder and more humid than those in year II. The hotter part of year II was also hotter than the corresponding part of year I at Jinja, as will be seen from data kindly supplied by the East African Meteorological Department at Entebbe (cf. Appendix 3).

The variation of the water temperature of Northern Lake Victoria is small. Fish (1957) recorded the temperatures at four different depths in the Buvuma and the Rosebery Channels from August 1952 till January 1954, and found that the temperature at the surface ranged from twenty-four to twenty-seven degrees centigrade. The temperature variations at the depths of ten, twenty-four, and thirty metres was the same, and varied from twenty-three and a half centigrade to twenty-six and a half centigrade.

Strong persistent wind is rarely experienced at Jinja. But bouts of strong wind, usually associated with rain showers and thunderstorms, do occur. Most of the wind is experienced during the day; the night is calmer in comparison. After sunset the wind generally subsides, but at times it reaches another maximum between 0200 hrs. and 0400 hrs. (East African Standard Time) due to local rainstorms and/or thunderstorms which tend to set in then. These rainstorms sometimes bring about a drop in the temperature, which on warm nights can amount to five degrees centigrade. The wind reaches its minimum at sunrise.

The general wind pattern outlined above is shown by the wind data recorded during year I and year II. In Fig. 7a and 7b the wind figures (in kilometres per hour) are shown (thin lines) against the time and the date when they occurred in year II. The wind data for year I are shown in Fig. 4 where the mean wind strength (in metres per minute) and the gmw wind values of the different ten minute sampling periods have been plotted against the time of the night. The second nightly wind maximum is evident from the plotting of the arithmetic means; but the second maximum is just discernible when the gmw-values are consulted (Fig. 4), showing that there is no consistency of results, *i. e.* that the second maximum was only experienced occasionally.

The periods of dusk and dawn are short. Adopting the definitions of civil twilight, nautical twilight and astronomical twilight as given in "The Nautical Almanac and Astronomical Ephemeris — — —" for 1957; civil twilight lasts for twenty to twenty-two minutes, the period of nautical twilight lasts for twenty-four to twenty-six minutes longer, and the astronomical twilight lasts for twenty-four to twenty-six minutes longer than the nautical twilight. The times of moonrise and moonset are of course related to the phase of the moon, but the times vary somewhat at a given phase of the moon (HARTLAND-ROWE, 1958). HARTLAND-ROWE (1958) has given further details in his paper, otherwise "The Nautical Almanac and Astronomical Ephemeris — — —" for 1956, 1957 and 1958 should be consulted.

The light intensity decreases rapidly at dusk and, on moonless nights, reaches its minimum period once the period of astronomical twilight is past. The light intensity remains at this minimum until the astronomical twilight of the morning sets in, and increases rapidly towards sunrise. Moonlight brings about "crepuscular" light intensities in the period of darkness — the intensity of the moonlight being dependent on the age of the moon, the height of the moon above the horizon, and the climatic conditions. The intensity of the moonlight is at its highest at full moon; at its quarters the light intensity of the moonlight is only twelve per cent of that experienced at full moon. (On some nights, flashes of light resulting from lightning, were not uncommon. No effect of these flashes on the flight activity was apparent.)

The light intensities as recorded by me, are given with every reservation. As mentioned, no suitable site was found for the photocell. Also, it proved impossible to get the lightmeter checked while in Uganda.

The light intensities on moonless nights showed the following range: Recorded five minutes after sunset: range 175 Lux — 17.5 Lux; fifteen minutes after sunset: 17.7 — 1.75 Lux; twenty-five minutes after sunset: 0.86 — 0.1 Lux; thirty-five minutes after sunset: 0.049 — 0.005 Lux; forty-five minutes after sunset: 0.006 — 0.001 Lux; and fifty-five minutes after sunset: 0.004 — 0 Lux. As the length of the night is less than twelve hours, the light intensity recorded in the last ten minute sampling period of the night is higher than the intensity recorded in the first sampling period of the night; the light intensity recorded in the last ten minute period but one, is higher than the light intensity recorded in the second ten minute period of the night — and so forth for all crepuscular sampling periods.

The highest intensity of moonlight recorded by me in year I was 0.32 Lux, recorded at a moon age of fourteen days.

The meteorological observations taken in year II have been sorted in lunar age groups and are presented in Fig. 5 and Fig 8. In Fig. 5 the mean temperature and the mean humidity at midday, at sunset and at sunrise are given for each moon age group. From the top of the diagram downwards, the humidities indicated (by dashed lines) are those of sunrise, sunset and midday. The temperatures (indicated by solid lines) are, from the top of the diagram downwards, those of midday, sunset and sunrise. The total number (n) of twenty -four hour cycles in each of the moon age groups is nine, excepting the moon age group of zero days where the number of cycles equals five. Rain has been plotted as the number of events — the term "event" meaning the number of observation periods (of a total number of nine or five — see above) when rain was experienced in each moon age group. No consideration has here been taken as to the amount of rain experienced. In Fig. 8 the mean wind strength (given in kilometres per hour) is plotted, for the four wind observation periods (see procedure), against the moon age.

As seen from Fig. 5 and Fig. 8, the meteorological factors: temperature, humidity, rain (events), and wind strength vary; but it is not possible to discern a "lunar periodicity" in the variation of these factors.

Before ending the present chapter, I want to mention that DDT has been put into the Victoria Nile in 1952 and in 1956. In 1956 the DDT was put into the river at the Owen Falls Dam. The result this had on the fauna below the Dam, has been mentioned by CORBET (1958b & 1958d), who showed that species of *Ephemeroptera* that bred below the Owen Falls were severely affected. The population at the Ripon Falls was left untouched, the Ripon Falls being upstreams from the Owen Falls Dam. A repopulation has since taken place below the Dam, presumably brought about by the down-stream movements of adults from the population left at the Ripon Falls (CORBET, 1958b).

Finally it should be mentioned that the level of the water between the Owen Falls Dam and the Ripon Falls has been raised. Before the Dam was built, the Ripon Falls were about fifteen feet high (MARTIN, 1956); in the early part of 1956 the falls had been reduced to a height of about a foot (CORBET, 1958b). Ultimately the former Ripon Falls will be completely submerged. This is bound to affect the insect fauna in the Ripon Falls, a fact already mentioned by HICKIN (1956).

Results

As there is no other feasible alternative, the *Ephemeroptera* fauna at Jinja must be recruited from larvae living in the Victoria Nile, in the lake itself and/or in the Napoleon Gulf area which lies between the lake proper and the Nile outlet.

The larvae thus live in waters that do not dry out during the dry seasons. And it is safe to assume that mayflies from both the river and from the Napoleon Gulf have been caught by the light trap.

We do not as yet know the larvae of all the different species mentioned in the present paper. Accordingly, in order to get an idea of where the larvae live, it is necessary to pool the available information. Published locality lists (Kimmins, 1948, 1956; Gillies, 1957a; Corbet, 1957, 1958b), observations on emergence and published studies on larval life are here of interest.

Corbet (1958b) has found larvae of *E. bugandensis*, *A. ugandanus* and *T. tinctus* in the Victoria Nile, and I have reared the two latter species from larvae collected below the Owen Falls Dam. *T. tinctus* is found in rapidly running water (Corbet, 1958b); the two other species have also been found at Entebbe (Kimmins, 1956) which suggests that their larvae may be able to exist in parts of the lake. Gillies (1957a), discussing some species of *Euthraulus*, states (*loc. cit.* p. 48): "*Euthraulus* appears to be the commonest Leptophlebiid to be found in small streams in East Africa, particularly at lower altitudes. It is far from being exclusively a torrential form.". Although larvae of *P. adusta* have been found in the Victoria Nile (Corbet 1958b), there can be no doubt that the swarms of this species experienced at Jinja are in the main recruited from larvae living in the Napoleon Gulf. Larvae of *P. adusta* are very common in the lake (Corbet, 1957; Hartland-Rowe, 1953).

I have observed *E. curtus*, *A. decoratus*, *C. corbeti*, *T. maculatus* and *P. adusta* emerging from the Napoleon Gulf. The species *E. bugandensis*, *H. fasciatus*, *C. notabile* and *C. dentatum* have not been observed emerging, nor is anything known concerning the larval habitat of the latter three. Corbet (1958a) assumes that the larvae of *C. notabile* live in rapidly flowing water and that it probably breeds at the Ripon Falls, and in the Victoria Nile below the Owen Falls. Jinja is the only locality where adults of *C. notabile* have been recorded (Kimmins, 1956). I have never observed *H. fasciatus* in nature, and it is rare in the catches (see Table II). Kimmins (1956) lists two localities where the adults of *H. fasciatus* have been taken: Jinja and Kaazi. To my knowledge there is no stream or river at Kaazi, and it is possible therefore that the species lives in the lake. Nothing can as yet be said about the larval habitat of *C. dentatum*. *T. maculatus* (adults) have been taken at Lake Nyasa (Kimmins, 1948); adults of *E. curtus* have been collected at Jinja and at Kaazi, and adults of *A. decoratus* have been found at Jinja, Ripon Falls and at Kaazi. It seems likely, therefore, that the larvae of *T. maculatus* and *E. curtus* at Jinja principally live in the Napoleon Gulf, and that the larvae of *A. decoratus* are to be found both in the Napoleon Gulf and in the Victoria Nile.

The total light trap catches of the different species of mayflies in year I and in year II will be found in Table II. In the table, I have doubled the number of *Ephemeroptera* identified and counted during year II (cf. Appendix 1).

The flight activity histograms of the different species of mayflies are presented in Figs. 9—19. The peak frequency histograms will be found in Fig. 22. An idea of the fluctuation of the nightly catches of various *Ephemeroptera* in year II can be obtained from Figs. 20—21 and from Figs. 23—35; and the catch/"lunar age" diagrams are given in Figs. 36—46. Observations on longevity are presented in Appendix 2.

Table II. *The catches (during the first hour of the night and the total catches) of some East African Ephemeroptera during year I and year II. N I and N II give the number of sampling nights in year I and year II respectively The table also*

Species	Sex	Stage	NI	NII	Numbers	
					Year I	
					First hour	Whole night
C. corbeti[1]	m.	i.	52	266	4	373
—«—	f.	i.	52	266		206
C. notabile	m.	i.	52	266	1,671	1,835
—«—	f.	i.	52	266	69,047	76,337
C. dentatum	m.	i.	52	0	6,604	10,790
A. ugandanus	m.	s-i.	52	266	206	245
—«—	f.	s-i.	52	266	79	88
—«—	m.	i.	52	266	1,103	1,249
—«—	f.	i.	52	266	8,271	9,577
A. decoratus	m.	s-i.	52	266	161	184
—«—	f.	s-i.	52	266	125	192
—«—	m.	i.	52	266	297	4,744
—«—	f.	i.	52	266	78	956
E. bugandensis	m.	s-i.	52	266	7,196	10,394
—«—	f.	s-i.	45	266	3,089	4,495
—«—	m.	i.	52	266	1,103	1,500
—«—	f.	i.	45	266	7,575	8,405
E. curtus	m.	s-i.	52	266	26,887	32,442
—«—	f.	s-i.	45	266	11,970	13,869
—«—	m.	i.	52	266	1	10,163
—«—	f.	i.	45	266		3,072
H. fasciatus	m.	i.	52	266		84
—«—	f.	i.	52	266		45
P. adusta	m.	both	52	266	317	2,645
—«—	f.	both	52	266	44	568
T. maculatus	m.	s-i.	52	266	351	400
—«—	f.	s-i.	52	266	271	313
—«—	m.	i.	52	266	1	59
—«—	f.	i.	52	266		20
T. tinctus	m.	i.	52	266		787
—«—	f.	s-i.	52	266		2,201

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[1] Three sub-imagines (females) found; they were caught during the first hour of the night.

gives the first hour catches as a percentage of the total catches. The mean catch per night, and the catch sex ratio expressed as the percentage of males, are listed for both years.

caught		First hour catch % of total		Mean catch per night		Catch sex ratio % of males	
Year II							
First hour	Whole night	Year I	Year II	Year I	Year II	Year I	Year II
42	2,246	1.1	1.9	7.2	8.4	64.4	71.6
	890	0	0	4.0	3.3		
3,092	3,594	91.1	86.0	35.2	13.5	2.3	2.9
104,114	118,326	90.5	88.0	1,468.0	444.8		
÷	÷	61.2	÷	207.5	÷		
2,796	3,444	84.1	81.2	4.7	12.9	73.6	72.6
1,162	1,302	89,8	89,2	1.7	4.9		
4,830	5,948	88.3	81.2	24.0	22.4	11.5	12.4
35,678	41,960	86.4	85.0	184.2	157.7		
1,716	2,108	87.5	81.4	3.5	7.9	48.9	44.9
1,848	2,588	65.1	71.4	3.7	9.7		
3,052	30,852	6.3	9.9	91.2	116.0	83.2	75.3
958	10,100	8.1	9.5	18.4	38.0		
25,952	38,040	69.2	68.2	200.0	143.0	66.7	66.0
13,426	19,618	68.7	68.4	99.9	73.8		
2,504	3,598	73.5	69.6	28.8	13.5	13.4	10.0
29,938	32,294	90.1	92.7	186.7	121.4		
90,106	116,960	82.8	77.0	623.9	439.7	66.9	67.2
45,662	56,928	86.3	80.2	308.2	214.0		
144	44,662	0	0.3	195.4	167.9	74.1	78.1
30	12,552	0	0.2	68.2	47.2		
2	434	0	0.5	1.6	1.6	65.1	70.7
2	180	0	1.1	0.9	0.7		
4,242	16,790	12.0	25.3	50.9	63.1	82.3	70.5
2,302	7,038	7.7	32.7	10.9	26.5		
1,734	2,180	87.8	79.5	7.7	8.2	56.1	49.3
1,838	2,246	86.6	81.8	6.0	8.4		
6	524	1.7	1.1	1.1	2.0	74.7	77.7
2	150	0	1.4	0.4	0.6		
	222	0	0	15.1	0.8	26.3	5.1
36	4,140	0	0.9	42.3	15.6		

It is evident from the flight activity histograms and the peak frequency histograms that most species dealt with here have their flight activity shortly after sunset and/or shortly before sunrise. This definitely holds good also for the rest of the *Ephemeroptera* caught by the light trap. Crepuscular flight activity patterns have already been reported in certain *Trichoptera* (CORBET & TJØNNELAND, 1955) and in two species of *Chironomidae* (TJØNNELAND, 1958b) at Jinja. The times of the flight *cum* feeding activity of certain insectivorous bats appear to coincide with the principal dusk and dawn flight activity peaks shown by the bulk of the nocturnal larvo-aquatic insects at Jinja. Similar feeding pattern in bats is mentioned by RAO & RUSSELL (1938) from India; additional references on the crepuscular activities of bats are listed by PARK (1940)

The flight activity histograms of the sub-imagines indicate that emergence takes place after sunset. I have never observed *Ephemeroptera* to emerge during the day at Jinja. Most — if not all — mayflies emerge between sunset and sunrise; a post-sunset emergence peak being very noticeable. The impressive evening emergence is easily observed from boats. During the nautical and astronomical twilights of the evening, the gulf is alive with emerging mayflies, caddisflies and *Chironomidae;* and surfacing shoals of fish, and a number of bats and crepuscular *Odonata* appear to take their toll of the emerging insects. Some mayflies, belonging to the genus *Caenis* and/or the genus *Caenodes* (referred to as "*Caenis-Caenodes*" sp. (spp.)), seemed to emerge in the morning, as very large numbers of sub-imagines occurred in the beginning of the morning peak. (It has been discussed whether *Caenis* exuviates in flight or not (BERNER, 1950; BURKS, 1953; EDMUNDS, 1956; LYMAN, 1955). The ones at Jinja were observed to settle, to moult in a few minutes' time and to swarm as imagines immediately afterwards.) Available flight activity histograms and peak frequency histograms for the sub-imagines of the species dealt with, reveal that the emergence of a species is not continuous during the night, but is restricted to a fixed short period of the early part of the night.

When employing a light trap and ten minute sampling periods in studying the flight activity of crepuscular insects, it is imperative to realize that the relative brightness of the mercury vapour bulb to its surroundings increases at dusk and decreases at dawn. Thus, optimal catching conditions may not for all species prevail during the period of maximum flight activity (cf. TJØNNELAND, 1958a). This will not — if dealing with crepuscular and nocturnal species — invalidate the flight activity histograms and the peak frequency histograms. Restricting the argument to the crepuscular species only, it means that the period of peak flight activity in the evening may slightly precede the period of the peak catch of insects. In the morning the reverse would be the case: the period of peak catch may precede that of peak activity. Working with ten minute sampling periods, an over-emphasis of the exact position (in time) of the peak catch sample may be erroneous and therefore inadmissible.

Kimmins (1955) mentions that *Cloëon* has been reported to swarm after sunrise in Nyasaland. As mentioned earlier, *C. dentatum* has been found to swarm after sunrise at Jinja. The flight activity histogram (Fig. 11) of *C. dentatum* (male imagines) may therefore be of interest, though the histogram only covers the flight activity between sunset and sunrise. According to Fig. 11, the male imagines of this species show a pronounced bimodal flight activity during the night; the only suggestion of a post-sunrise activity is found in the fairly high gmw-value (0.45 individuals per night) for the last ten minute sampling period of the night. In the remaining ten species, not known to fly after sunrise, the corresponding gmw-values are much lower.

In dealing with the other ten species, it is possible to discern between three groups. The first group (group I) consists of the species that complete their active adult life cycle (but not necessarily the whole adult life) in twelve hours or less. Group III consists of the species that complete their active adult life in twenty-four hours or more. Group II contains the species where a proportion of a single emergence group completes its active life cycle during twelve hours or less, and where, as a regular feature, the remaining proportion needs twenty-four hours or more to complete its active life cycle. As noticed, group II is merely an intermediate group between the other two. The classification in the three groups mentioned is devised more for practical than for logical reasons. *E. curtus* is a typical representative of group I, and will be dealt with in some detail below.

E. curtus emerges at dusk and the sub-imagines fly immediately afterwards. The evening flight activity is very pronounced and consists almost exclusively of sub-imagines (Fig. 16a & 16b). Once the evening peak has been reached, the decline of the evening peak is at first rapid, but the activity of the sub-imagines continues at a low level for a substantial part of the night. The few sub-imagines caught late at night probably represent late emergers. The rapid decline of the peak is probably the result of two phenomena. The trap itself removes part of the flying population, but although the trap is efficient and despite the fact that various predators take their toll, it is felt that this "removing" factor is of little concern to the numerical size of the population of insects. The principal reason for the rapid decline is that the sub-imagines become quiescent. As seen from Fig. 22, the peak dispersion of the evening activity peaks (*i. e.* the sub-imaginal peaks) is small. The sub-imagines moult during the night and fly as imagines the following morning. Although mating has not been observed, the morning flight is bound to be the mating flight. Few imagines (all males) have been caught in the evening peak, and it is inferred that most of the imagines die off in the morning and during the day. The species shows a bimodal flight activity with a dusk and a dawn peak.

The onset of the imaginal peak is not as abrupt as that of the sub-imaginal peak (Fig. 16a & 16b). The flight of the imagines of one particular emergence group cannot, of course, start before at least some of the sub-imagines have completed the ecdysis and are ready to fly. Moulting being a temperature dependent process, the times of the beginning of the imago flight activity and the time of the flight activity peak could well be presumed to vary with the temperature of the night. These problems, therefore, need some consideration. In Fig. 47, the time when the first imago (or imagines) was caught after the first two hours of the night has been shown against the temperature at midnight. It is clear from Fig. 47, that there is a relation between the catch of the first female imago of *E. curtus* and the temperature at night, as expressed by the midnight temperature. For the males, the picture is less clear; the dispersion — within each of the different temperature groups — of the times of the first arrivals of the male imagines being much wider. This could lead to the conclusion that the influence of temperature on moulting was far greater in the males than in the females; but I do not believe this to be correct. The dispersion is probably brought about by having, on occasions, male imagines from two successive emergence populations flying on the same night. The very early first catches of male imagines would then be the catches of imagines that have been quiescent during the day. It is, unfortunately, not possible to predict where the dividing line between the two age groups of male imagines is to be found in Fig. 47. While the times of the first captures of female imagines (and probably also of the male imagines) are to a great extent dependent on the temperatures experienced on the various sampling nights in year I, and while the start of the build up of the imago flight activity peak of the morning is also thus affected, the actual times of the flight activity peaks themselves vary little (Fig. 22). The peak dispersion of the morning peaks (Fig. 22) seems wider than that of the evening peak. The morning peak dispersion, as shown in Fig. 22, is partly an artefact. Thus the peaks (or events — see Procedure) registered before the periods of morning twilight, are those for the nights when unfavourable climatic conditions prevailed during the ordinary peak catch periods of *E. curtus*.

The times of the last captures of sub-imagines of *E. curtus* show no evident relation to the temperatures of the different sampling nights in year I. The late catches of sub-imagines mainly occur on nights when these insects, as judged from the evening peak catches, are particularly abundant.

Returning to the flight activity histograms once more, it is clear that some of the flight activity of *E. curtus* takes place outside the twilight hours. Worthy of notice in this connection are the facts that moonset and moonrise did not trigger off bouts of flight activity, nor did the intensity of the moonlight appear to stimulate or prolong the flight activity periods of *E. curtus.*

In *E. curtus* the population of imagines flying at dawn is, as seen, recruited from the insects that have emerged and flown as sub-imagines at dusk. The two adult stages of the emergence group fly under different climatic conditions (apt to vary somewhat from one night to the next). This affects the numeric size of the catches in various ways; but on the whole the numeric size of the catch of imagines should bear a strong relationship to the catch of sub-imagines of the same emergence population. If Fig. 34 & Fig. 35 — giving particulars of the catches of imagines and sub-imagines of *E. curtus* over the 266 nights in year II — are consulted, it is found that the catches of the two stages vary in concert.

It is obvious from Figs 34—35 and from the data collected during year I, that *E. curtus* does not show any seasonal emergence at Jinja. Nor do these two figures suggest any lunar rhythm of emergence in this species. The "mean catch/lunar age" diagrams (see Procedure) in Figs. 39 & 40 are decisive on this point. Although the catches of both male and female imagines rise to a peak shortly after full moon, the same tendency is not very pronounced in the sub-imagines. CORBET (1958c) failed to find a lunar periodicity of emergence in *E. curtus;* and his finding is thus confirmed.

In nightly light trap catches the lowest number of insects are often caught at, or around, full moon. It has been suggested (WILLIAMS, SINGH & EL ZIADY, 1956) that the reason for this could be that the high intensities of moonlight decrease the relative brightness of the mercury vapour bulb. Populations flying for short periods at dusk and dawn would here be differently affected, as mentioned by TJØNNELAND (1958b); but *E. curtus* does not really conform to the expected pattern in this respect. Nor does the species show the criterion: a trough of the sampling means at, and near, full moon. It seems unlikely, therefore, that moonlight significantly reduces the catches of *E. curtus* even around full moon. Such an effect could, however, be masked, and compensated for, by large populations emerging at, and near, full moon. On the whole it seems likely that catches of crepuscular species would be less affected than catches of non-crepuscular nocturnal species by the light intensity of moonlight.

In addition to *E. curtus* and "*Caenis-Caenodes*" sp. (spp.), *T. maculatus, T. tinctus* and *P. adusta* belong to group I. This is probably also the case for *C. corbeti.* And it seems possible that *H. fasciatus* does also belong to the same group.

T. maculatus was caught regularly by the trap, but never in great numbers (Fig. 24—25). The species did not show any seasonal distribution, nor did it show a lunar periodicity of emergence (Figs. 38a & b), but the mean values show a trough near full moon. The species emerges shortly after sunset and the flight activity corresponds to that of *E. curtus* (Fig. 17), the peak dispersion (Fig. 22) of the morning (*i. e.* imaginal) peak being wider than that of the evening (*i. e.* sub-imaginal) peak. *T. maculatus* moults during the night and appears to show the same relationship between the time of moulting and the temperature as does *E. curtus.*

Neither *C. corbeti* nor *H. fasciatus* have ever been taken in great numbers by the light trap; but both species are commonly represented in the nightly catches (Fig. 21 & Fig. 23). Imagines of both species are mainly found in the morning peak (Figs. 9 & 12; Table II; Fig. 22). Although imagines of *C. corbeti* are mainly caught at dawn, male imagines have been taken at dusk. Single sub-imagines of this species were taken during the first sampling hour on three different nights in year II. I have also observed sub-imagines (both sexes) of *C. corbeti* to emerge after sunset at a locality marked * in Fig. 1. I assume therefore, that the species shows the same flight activity pattern as does *E. curtus,* and that the male imagines found to fly in the dusk peak are those that have survived the day. Why so few sub-imagines of *C. corbeti* have been caught by the trap, is not quite clear. It is of course possible that the sub-imagines are not strongly attracted by the mercury vapour light, but this explanation need not apply. It is quite possible that the flight activity of the sub-imagines is of such a short duration, when compared to the distance the sub-imagines have to fly in order to reach the trap, that only chance captures can be expected.

C. corbeti and *H. fasciatus* do not show any seasonal emergence, nor do they show a lunar periodicity of emergence. In Fig. 23 the numbers (expressed as log (n + 1) see Procedure) of male imagines of *C. corbeti* caught during the first hour of the night have been indicated by cross-lined areas. It is worth noticing that these captures do not show a relation to the wet season, a relation one would expect. But the captures do tend to lag twelve hours (a day) behind peak morning catches of male imagines, indicated by solid black areas in Fig. 23.

It is not yet possible to form any definite opinion as to the flight activity pattern of *H. fasciatus.* Sub-imagines have never been taken, nor are they known. The reason why none have been taken by the trap could be the same as suggested for *C. corbeti.* The possibility can not be excluded that *H. fasciatus* emerges during the day or/and that it does not have a sub-imaginal flight activity at all. The flight activity of *H. fasciatus* shows some resemblance with that of *C. corbeti,* and I have therefore — with some doubt — incorporated *H. fasciatus* in group I. The times of the first captures of the imagines in the morning peak bear no relation to the temperature of the night in *C. corbeti* and *H. fasciatus,* but the latter species is more often met with on warmer nights. As seen from Figs. 9 & 12, a gradual build up of the dawn peaks appears to be absent. This may not be so in nature. As only a few specimens of the two species were caught by the trap in any one night, it is rather likely that the trap was situated in the periphery of the effective flying area of the species. The two flight activity histograms would then be expressive of the maximum flight activity periods, representing approximately the topmost part of a hypothetical flight activity histogram looking much like that of *E. curtus.*

The flight activity of *T. tinctus* and *P. adusta* differs strikingly from the pattern presented by *E. curtus, T. maculatus, C. corbeti* and — possibly — *H. fasciatus.*

T. tinctus is a torrential species, having been found at the Ripon Falls and at the Owen Falls (CORBET 1958a). The larvae develop in about ten weeks or less (CORBET 1958b). The adults are a great nuisance at the Owen Falls Dam, and are most likely the mayflies referred to by BERTLIN & OLIVIER (1954) — see Introduction. As the highway between Jinja and Kampala —Entebbe crosses the Victoria Nile at the Owen Falls Dam, the nuisance created by swarms of *T. tinctus* has been experienced by many. The nuisance is hardly felt during the first couple of hours after sunset, although other troublesome larvo-aquatic insects (*Cheumatopsyche copiosa* KIMMINS, *Phanostoma senegalense* BRAUER (*Trichoptera*) and others) are of course active at the Dam at this time. The swarms of *T. tinctus* are mainly experienced from about 2200 hrs. to a few hours after midnight. The number of *T. tinctus* flying at the Dam varies from night to night; very heavy swarms are reputed to occur at irregular intervals, showing no seasonal pattern. The emergence of this species does not show a lunar periodicity.

Larvae of *T. tinctus* have never been taken in the Napoleon Gulf, and it is indeed unlikely that the species breeds there. The nearest emergence site (as seen from the light trap) is thus the Ripon Falls. Considering the distance between the emergence sites and the insect trap, it is noteworthy that the flight activity histograms (Fig. 19) supply reliable information on the swarming activity of this species. The peak dispersion is considerable (Fig. 22). The wide peak dispersion is probably the result of nightly variations in climatic conditions (wind strength and direction being important) working on populations that fly for a relatively long period per night, and that have originated from places relatively far from the place where individuals of the flying population are collected.

The males of *T. tinctus* collected by the light trap have been imagines. Studies at the Owen Falls Dam indicated that the male sub-imagines start emerging shortly after sunset. They do not seem to be particularly active in this stage, but settled immediately after emergence, which may explain why none have been taken by the light trap. In nature, males have been observed to moult between two and a half to three hours after sunset, taking off within a couple of minutes after the exuviation had taken place. The ecdysis of the male is a complete one.

All the females examined have had a partial fringe of hairs along the anal margin of the wing. KIMMINS (personal communication) has found the same in the females of *T. tinctus* examined by him, yet some of these were without doubt sexually mature as they carried egg masses attached to the abdomen. This indicates that if the females of *T. tinctus* moult at all, they probably only undergo a partial ecdysis. Nor has CORBET (personal communication) seen female imagines of this species. Considering the available information, I find that we have no positive evidence to the effect that the females of *T. tinctus* undergo a complete ecdysis — if they indeed undergo an ecdysis at all.

The females of *T. tinctus* have not been observed emerging. The possibility exists that they emerge together with the males, but that they keep sitting about until they take off a few hours later. I consider this to be unlikely, as I have never found female sub-imagines at this time. I find it more likely that the females emerge later than the males, and that they start their flight at the time when the males have completed exuviation. The appearance (in time) of the swarms — consisting to a greater extent of females — lends support to this view.

Few — if any — adults of *T. tinctus* survive to fly on a second night.

CORBET (1958a) writes that *T. tinctus* tends to appear at light at Jinja in very large numbers at short, irregular intervals, and suggests that the occurrence may be influenced by the fluctuation in the amount of water passing over the Ripon Falls. CORBET (1958a) is probably right in assuming that the high numbers caught by the trap during his experiments, have arrived mainly from the Ripon Falls. The number of powerful streetlamps found between the E.A.F.R.O. laboratory and the Owen Falls Dam, as well as on the Dam itself, would attract a great proportion of the insects emerging at the Dam, and make it very difficult for a great number of insects from the Owen Falls Dam to arrive at the trap. The submerging of the Ripon Falls was probably responsible for the fact that I did not get very large nightly catches of *T. tinctus* during my experiments. It probably also explains why the nightly mean catches of *T. tinctus* were smaller in year II than they were in year I (Table II). It is evident from Table II that the catch sex ratios (per cent of males) are very different for the two years. The nightly catch sex ratios vary a great deal, as gathered from Fig. 20, and the explanation for the yearly differences could be that the data collected during year I were biased. But even the yearly differences in catches sex ratios may partly lie with the submerging of the Ripon Falls. In *T. tinctus* the females are much more robust than the males (KIMMINS, 1956), and it is reasonably presumed that the females have the greater dispersion potential. If then a proportion of the catches of *T. tinctus* is recruited from the population at the Owen Falls, this proportion is likely to show a disproportionately high percentage of females. A decrease in the emergence populations at the Ripon Falls could thus bring about a noticeable difference in catch sex ratios.

No seasonal distribution pattern is evident from my trapping data (Fig. 20), but the catches of *T. tinctus* have been low around full moon (Fig. 43). This could be caused by the high intensities of moonlight at that time.

The larvae of *P. adusta* are wood-borers (KIMMINS, 1948), as are the larvae of a related species, *P. corporaali* LESTAGE, in Asia (ULMER, 1939; VEJABHONGSE, 1937). The larvae of *P. adusta* seem to develop in four to five months (CORBET, 1957). The biology of this species has been studied by HARTLAND-ROWE (1953, 1955, 1958), who found that the species shows a lunar rhythm of emergence from Lake Victoria, that the emergence takes place between 1930 hrs. to 2100 hrs. (East African Standard Time), that the individuals exuviate on the wing and that the adults only survive for about an hour. The lunar periodicity of emergence has since been confirmed by CORBET (1958c) and is also confirmed by the data here presented (Figs. 27 & 42). The species does not show any seasonal distribution pattern.

HARTLAND-ROWE'S (1958) observations on the flight activity of *P. adusta* have also been confirmed (Fig. 18). As the nightly catches of *P. adusta* exhibit a gradual series where individuals in all stages of moulting are represented, no attempt has been made to record sub-imagines and imagines separately in the present study. It is evident from Fig. 22 that the peak dispersion histogram presents a somewhat vague picture. This is probably brought about by having the sub-imaginal and the imaginal flight activity encompassed within one flight activity peak.

The catch sex ratios vary a great deal from night to night in *P. adusta.* And the onset of the flight activity appears not to be quite as well fixed according to the times of sunset as in some of the other species already dealt with. But, as the sampling during year I was not carried out nightly, the available data are too few to merit an analysis on this point.

Group II contains only *A. decoratus.* The flight activity bears a strong relationship to that of *E. curtus*, inasmuch that the insects emerge shortly after sunset; they fly as sub-imagines in the dusk peak, they moult during the night and they fly as imagines in the dawn peak. A fair number of the imagines survive the day to fly in the following dusk peak. They fly somewhat earlier than the sub-imagines of the successive emergence population (Figs. 14a & b). The possibility that some insects survive to fly in a second dawn peak can not be excluded. As seen from the two figures mentioned, a gradual build up of the dawn peak is recognizable, yet the peak dispersion is small (Fig. 22) — the isolated single peak catches recorded in Fig. 22 stem from aberrant climatic conditions as mentioned for *E. curtus*.

The build up of the morning peak starts before the onset of the astronomical twilight, and it is not unreasonable to presume that the times of first arrival of the newly moulted imagines in the trap would show a relation to the temperature of the night. For *A. decoratus* this is impossible to demonstrate from the catch data, as the newly moulted imagines could not be discerned from those originating from the previous emergence group.

The imagines of *A. decoratus* flying in the evening, are likely to have been recruited from two different categories of the same emergence population. The first category comprises those that have moulted sufficiently early to have taken part in the dawn flight — and may, or may not, have done so. The second category contains those that have not moulted early enough to take part in the dawn flight activity at all. It is, namely, reasonably assumed, that the "exuviation" curve (the number of insects of an emergence population exuviating as plotted against the time when the exuviation is completed and the insects are able to fly) would be a normal — or skew — distribution curve, *i. e.* a curve that shows one maximum and trails off at both ends. Should the right hand end of this curve trail off past sunrise, the insects then ready to fly would be flight inhibited. When able to survive the day, these insects that have undergone ecdysis so late would fly the following evening. The lower the temperature, the more insects would exuviate late and be unable to take part in the dawn flight, and the greater number of imagines would be expected to be caught the following evening — under otherwise identical climatic conditions. As I have not succeeded in getting *A. decoratus* to complete its moult in captivity, the explanation provided above is at present largely hypothetical.

The numeric size of the captures of *A. decoratus* on the different nights in year II, can be found from Figs. 30 & 31. The catches of imagines taken during the first sampling hour of the night (i. E. = imagines: evening) are indicated by cross-lined areas; the catches of the imagines taken during the other eleven hours of the sampling nights (i. M. = imagines: morning) are shown by solid black areas. As gathered from the flight activity histograms (Figs. 14a & b) it seems certain that the i. M.-catches would contain imagines from two different emergence groups and probably be of a more heterogenous nature than the i.E.-catches. It does not seem particularly likely namely, that *A. decoratus* imagines would be able to survive two tropical days in nature. As the older lot of imagines would in general be in a minority in the i.M.-catches, the division into the i.E.- and i.M.-catches is sound. In Figs. 30 & 31, one would expect the catches of sub-imagines and the i.M.-catches to vary in concert, and it is further expected that the i.E.-catches of night number z + 1 would vary with, and be related to, the catches of sub-imagines (and the i.M.-catches) of night number z. These tendencies are also evident in Figs. 30 & 31. As the i.E.-catches and the catches of sub-imagines caught on identical nights represent catches of two different emergence populations, one would not expect these catches to vary in concert. But the latter expectation is not quite fulfilled. The reasons for this, are not difficult to fathom. They are without doubt mainly climatical.

First of all, sub-imagines and imagines (i.M.) from the same emergence group — flying on identical nights — fly under climatical conditions that are 1) hardly ever identical and 2) variable from night to night. Whereas the two unrelated populations: i.E. resulting from insects that have emerged on night number z and the sub-imagines that have emerged on night number z + 1, both fly — and are captured — in the evening of night number z + 1. As the time difference between their flight activities is negligible, they fly under climatic conditions that are usually very similar. The fact that the catches of these two populations show some similarities, is therefore not surprising. Secondly, the climatic conditions prevailing during the whole of the night are also of importance, and they may vary considerably from one night to the next. Thirdly, the climate experienced during the day is of paramount importance. As seen, in *A. decoratus* the i.E. fraction of the population has survived the tropical day, and it would seem that the humidity during the day would play an important part in determining the chances of survival. This has been demonstrated in Table III below.

Table III.

rH% at midday, (range)	Number of events (n)	Arithmetic mean half catches of *A. decoratus* (i. E.)	
		males	females
30—39	17	2.59	0.47
40—49	55	4.13	0.96
50—59	80	6.18	2.26
60—69	72	6.54	1.24
70—79	34	8.09	4.24
80—89	5	0.80	0.60
90—99	3	3.67	0.33

In Table III the arithmetic mean catches (per night) of i.E. of *A. decoratus* are listed against the humidity recorded the previous midday. The means given are those for year II, and are the means for approximately half the catches, that is the insects found in the set of two chambers (see Procedure).

In Table IV, the arithmetic mean half catches (per night) have been listed against the humidity recorded at sunset. Otherwise as in Table III.

Table IV.

rH% at sunset, (range)	Number of events (n)	Arithmetic mean half catches of *A. decoratus* (i. E.)	
		males	females
40—49	2		
50—59	17	1.88	1.12
60—69	61	5.41	1.13
70—79	133	6.17	1.70
80—89	47	7.15	3.36
90—99	6	1.33	1.17

Thus nights following days with a low humidity show low catches of imagines of *A. decoratus* during the first hour of the night. The catches tend to increase with increasing day humidities — up to a point. At very high day humidities, the catches of *A. decoratus* imagines in the evening are again low. It should be made clear, however, that the highest day humidities are the result of violent rains (and a drop in temperature) during the day. Violent rain is probably in itself detrimentary to the population of imagines, and often results in a low evening temperature which in *A. decoratus* seems to impair flight activity. As it is so difficult to resolve the effect of the different single climatic factors on flight activity, it is possible that a high day temperature — which always prevails on days with a low humidity — may in itself have a somewhat detrimental effect on the population surviving the day.

From Figs. 30—31, and from the records from year I, it is evident that *A. decoratus* shows no seasonal pattern of occurrence. Catches of sub-imagines and of imagines flying in the morning (i.M.) have been fairly steady. But, as would be expected, some seasonal effect is noticed as far as the catches of imagines in the dusk peak (i.E.) are concerned. The catches of i.E. have been higher in the wet season than they were in the dry season.

The mean catches of *A. decoratus* sub-imagines and dawn imagines (i.M.) show a maximum around and after full moon with a trough before full moon (Figs. 45a & b). This may be an indication of a lunar periodicity of emergence, but as the pattern is variable and far from being a clear cut one, I consider a claim for a lunar periodicity of emergence in *A. decoratus* to be premature.

The remaining three species: *A. ugandanus, E. bugandensis* and *C. notabile* belong to group III. It is likely that these species emerge shortly after sunset, but *A. ugandanus* is the only species which has been observed doing so.

The sub-imagines of *A. ugandanus* fly towards the end of the ordinary dusk peak and show no other activity peak for the rest of the night. The exuviation takes place on the following day and the imagines fly in the following dusk peak — somewhat earlier than the sub-imagines of the successive emergence population. The flight activity curve is a curve of exhaustion, part of both the sub-imaginal and the imaginal flight activity taking place outside the twilight hours (Figs. 13a & b). The imagines show a minute flight activity peak at dawn which has not been indicated in the peak frequency histogram (Fig. 22). This dawn peak results from a very small number of insects (twenty-eight in all) being taken on five nights in year I; the recorded dawn temperatures were: 17°C, 18°C, 19°C, 20°C and 20°C. Only four *A. ugandanus* imagines were found in the dawn peaks on the three nights when the dawn temperature was below 20°C, against twenty-four individuals on the two nights when the dawn temperature was 20°C. It appears that the negligible dawn peak is dependent on at least two factors: 1) a heavy influx of *A. ugandanus* (imagines) in the evening peak, 2) a fairly high temperature. The imagines flying at dawn are not likely to have been recruited from the sub-imagines of *A. ugandanus* flying in the beginning of the night as these moult well after sunrise (see Appendix 2). The imagines active at dawn must therefore stem from the population (or populations) of imagines that have been active in the evening peak. Thus, the imagines of *A. ugandanus* flying in the evening are, at least to some extent, comparable with the i.E.fraction (see above) of *A. decoratus;* but the dawn flying imagines of *A. ugandanus* are not comparable with the i.M. fraction of *A. decoratus.* A comparison is given below.

A. decoratus: s.-i. — — — i.M. — — — i.E. — — — i.M.$^{\mathrm{I}}$(?) — — —(?)
A. ugandanus: s.-i. — — — — — — — — i.E. — — — i.M.$^{\mathrm{I}}$ — — — i.E.$^{\mathrm{I}}$(?)

That the i.M.$^{\mathrm{I}}$ individuals should be the last and only survivors of their emergence group is not likely as they are found on rather warm mornings. It is far more probable that they represent a small active fraction of a larger but mainly inactive i.M.$^{\mathrm{I}}$ population, a population kept inactive because of the general low temperature at dawn. HADDOW (1956) suggests that the low temperatures at dawn are responsible for the fact that the dawn biting activity peak is smaller than the dusk peak in certain mosquitoes. As far as it is possible to draw conlusions from the longevity experiments, these indicate that *A. ugandanus* under favourable conditions in nature may well survive to fly as an i.E.$^{\mathrm{I}}$ fraction. The peak dispersion of *A. ugandanus* is small (Fig. 22).

A. ugandanus shows no lunar cycle of emergence (Figs. 41a & b). The results of the continuous catches in year II are given in Figs. 28—29. These results and my catch records from year I show no seasonal pattern of occurrence in this species. *A. ugandanus* having no i.M. fraction, the first imagines of an emergence group that are caught by the light trap are those (i.E.) that have survived a tropical day. Accordingly the catches of imagines would be expected to be small on evenings following dry days and hence to diminish in the dry seasons. And when studying Figs. 28—29 one would — climatic considerations apart — expect the i.E. catches of night number z + 1 to vary with, and be related to, the catches of sub-imagines on night number z. Also since *A. ugandanus* may well survive to fly as i.E.^{I}, one would expect a gradual decline of the catches since the catches of i.E.^{I} on night number z + 2 would be related to the catches of i.E. imagines on night number z + 1.

The expected tendencies, outlined above, are discernible in the data collected. Compared with the catches of imagines of *A. ugandanus*, the catches of sub-imagines are somewhat irregular; suggesting that the flight activity period of the sub-imagines is one of shorter duration. Thus catches of sub-imagines should be indicative of large emergence groups. And as seen (Figs. 28—29), the peak catches of sub-imagines, though irregular in appearance, in general precede peak catches of imagines. Further, the catches of imagines are somewhat reduced on evenings following dry days. As far as the dry seasons are concerned, the picture is less clear, this presumably being brought about by the fact that there are no really typical dry seasons at Jinja. My catch data for *A. ugandanus* seem to suggest that peak emergence has often followed days and/or nights with rain.

If the catch sex ratio of the sub-imagines of *A. ugandanus* is compared with that of the imagines, a striking fact emerges (Table II). The males predominate in the catches of sub-imagines, whereas the females predominate in the catches of imagines; and the catch sex ratios are approximately the same for the two years. The reasons for the difference between the catch sex ratio between sub-imagines and the imagines of *A. ugandanus* are not known. The most likely explanation is that the female sub-imagines are less attracted by the trap than are the male sub-imagines, but this is by no means the only explanation that could be launched to explain the difference in sex ratios. Further investigations will however be required before the question can be satisfactorily solved. Whatever the reasons, the phenomenon mentioned is one of considerable interest, as it is only found in group III. In the species belonging to group I and II, the imagines that survive the tropical day are nearly all males. Of the remaining two species in group III, the decrease of the catch sex ratio (percentage of males) from sub-imagines to imagines is also found in *E. bugandensis*. In *C. notabile* the sub-imagines were not recorded, but the females predominate in the imagines catch (Table II).

The flight activity of *E. bugandensis* resembles that of *A. ugandanus*, but *E. bugandensis* imagines show no dawn activity peak (Figs. 15a & b). The peak dispersion (Fig. 22) is small; as in the other species dealt with, the isolated peak catches do not signify a change in flight activity.

At Jinja the sub-imagines of *E. bugandensis* usually moult during the first couple of hours after sunrise, which can be readily tested by isolating sub-imagines from the evening peak in the open. See also Appendix 2. The sub-imagines will however moult before sunrise if kept at a temperature higher than the ordinary night temperatures experienced in the open. The sub-imagines of *E. bugandensis* thus moult later than those of *E. curtus*, a fact that can be observed by examining the sub-imagines of *Euthraulus* found at sunrise and during the first couple of hours after sunrise. Sub-imagines of *E. curtus* (group I) are never found at this time, whereas sub-imagines of *E. bugandensis* are often found. The sub-imagines of *E. bugandensis* moult earlier than the sub-imagines of *A. ugandanus;* nevertheless they generally moult too late to fly in the morning peak as imagines. It seems likely from the longevity experiments that some imagines of *E. bugandensis* may survive the night to fly in the dawn peak, yet that does not happen. The existance of an i.E.^{I} fraction seems unlikely in *E. bugandensis.*

E. bugandensis shows no real seasonal pattern of occurrence (Figs. 32—33), nor does the species show any periodicity of emergence from Lake Victoria (Figs. 46a & b). As would be expected, the catches of imagines are reduced on evenings following dry days, and the peak catches of sub-imagines tend to precede the peak catches of imagines by one day (Figs. 32—33).

The flight activity histogram of *C. notabile* imagines is given in Fig. 10. The species shows a bimodal activity with a very pronounced evening peak and a minute, but discernible, morning peak. As in *A. ugandanus* dawn peaks are experienced on warm mornings following high evening catches of the species. The peak dispersion of *C. notabile* is moderate (Fig. 22), the isolated peak catches are not indicative of changes in flight activity.

The sub-imagines of *C. notabile* could not be dealt with in the present study. The sub-imago stage has not been described, and could not be recognized and identified by me. The longevity of the imagines indicates that the sub-imago stage lasts for a fairly long time (probably twelve hours or more). The longevity, the flight activity pattern and the fact that the females strongly predominates in the catches of imagines (percentage of males: 2.3 (year I), 2.9 (year II) — see Table II) strongly suggest that *C. notabile* naturally belongs to group III. The relation of the evening catches to the humidity experienced during the previous day also points in this direction. I suppose therefore that the first active imaginal fraction of *C. notabile* is an i.E.-fraction with a small i.M.^{I}-fraction in the following dawn peak — not excluding the possibility for an i.E.^{I} activity. If the assumption is correct, the activity pattern of *C. notabile* would closely resemble that of *A. ugandanus.*

The percentage of males in the catches of imagines (cf. page 37) is very low in *C. notabile.* It is possible that the species is largely parthenogenetic; parthenogenesis has been described in *Centroptilum* (DEGRANGE, 1954). Further research will be needed, as the catch sex ratio proves little. Stratification of the flight levels brought about by different temperature preferences of the sexes (as described by WELLINGTON (1944) for mosquitoes) may play a part in determining the catch sex ratio at ground level, but a possible stratification can hardly be held wholly responsible as it would fail to explain the consistently low catches of males experienced in *C. notabile.*

C. notabile shows no lunar periodicity of emergence from the lake (Fig. 37) and it shows no seasonal emergence (Fig. 26).

In Table V (page 39) are listed the total catches of each of the species, excepting *C. dentatum,* in six fractional nightly samples. In these experiments the trap was switched on at different times each night and left to collect insects until sunrise the following morning. It will be noticed that the trap was switched on after the evening peak had subsided, hence the low catches of sub-imagines. And few — if any — imagines of the species that have a pronounced imaginal evening peak were taken. Table V shows that the decline in number of sub-imagines — as well as in certain imagines — after the dusk peak, is not the result of a progressive depletion of the population by the trap. And the table confirms our concept of the flight activity of the species involved.

It has become clear from the flight activity studies that variable climatic conditions, moon-rise, moonset or moonlight intensity do not alter the flight activity pattern of the species studied. The flight activity of the *Ephemeroptera* concerned is therefore a rhythmic one. Some of the flight activity patterns shown by single emergence groups of some of the species have been presented in a simplified form for comparison in Fig. 50. In this figure the approximate duration and the active and quiescent phases of the sub-imaginal and imaginal stages have been shown, the sub-imaginal stage by means of dashed lines, the imaginal stage by means of solid lines. For *T. tinctus* females (see page 30) a dotted line has been employed. Two slightly different alternatives have been given for *A. ugandanus.*

Although the environmental factors, within the variation limits experienced at Jinja, do not alter the flight activity pattern, they do have an important bearing on the numeric size of the catches during the activity periods of the

Table V. *Number of insects caught in six fractional nightly samples. Times given in E.A. Standard Time.*

Species, sex and stage	Sunset time:					
	1855	1855	1855	1855	1855	1842
	Trapping started:					
	2010	2215	0015	0215	0415	0515
C. corbeti m. i.	26	10	2	2	2	4
—«— f. i.	8	10				1
C. notabile m. i.						
—«— f. i.						
A. ugandanus m. i.						
—«— f. i.				2	4	
—«— m. s.-i.						
—«— f. s.-i.						
A. decoratus m. i.	304	104	212	138	50	96
—«— f. i.	40	2	6	12		48
—«— m. s.-i.		2				
—«— f. s.-i.	2		2			
E. bugandensis m. i.						
—«— f. i.						
—«— m. s.-i.						
—«— f. s.-i.						
E. curtus m. i.	346	30	148	198	76	645
—«— f. i.	54		32	28	12	[1]
—«— m. s.-i.	40		8			
—«— f. s.-i.	8					[1]
H. fasciatus m. i.	6	2				
—«— f. i.						
P. adusta m. (i. + s.-i.)						
—«— f. (i. + s.-i.)	2					
T. maculatus m. i.	6	2	6	8	2	3
—«— f. i.	2			2		1
—«— m. s.-i.	4					
—«— f. s.-i.	2					
T. tinctus m. i.						
—«— f.[2]	24					

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[1] Females not identified.

[2] See page 30.

different species. These catches may be severely reduced — or even obliterated — meaning that severe climatic conditions may prevent an activity peak, or prevent the activity peak from being expressed in the experimental design employed in the present study. But the climatic conditions do not create new subsidiary peaks in this case.

External factors may affect the catches in the trap in many ways, they may affect the size of the emergence group, and may reduce the size of the emergence group, be the climatic conditions severe when the emergence is actually taking place. External factors may reduce the size of the sub-imaginal and the imaginal populations. By delaying moulting, external factors will to some extent determine the number of imagines capably of flying once the proper activity period (periods) of the species sets in. External factors will also determine the size of the active proportion of the population and the intensity of its activity during the flight activity periods of the species. And, external factors will also influence the number of insects caught by the light trap. The effect of the external factors on the populations and on the catches in the traps, is an exceedingly complex and involved problem. In the present study it is not possible to separate the different components of this problem from each other. It is thus not possible to provide more than a few general statements. In spite of obvious short-comings, these statements should nevertheless be of value.

Wind strength has an important bearing on the catches of various insects in the mercury vapour trap, as demonstrated by WILLIAMS (1940); CORBET & TJØNNELAND (1955); SYLVÉN (1958) and TJØNNELAND (1958a & b). This can be ascertained by visual inspection alone. The cloud of insects that forms around the mercury vapour bulb on calm evenings at Jinja disperses when squalls of strong wind are experienced.

TISCHLER (1949) refers to the flight activity of mayflies under different wind velocities (*loc. cit.* p. 139): "Eintagsfliegen werden bei einer Windgeschwindigkeit von 6 m/sec erfasst und weggetrieben, bei 3 m/sec fliegen sie noch aktiv umher.".

During the mayfly peak activity periods at night at Jinja, wind velocities of six metres (or more) per second were not recorded at the site of the trap, and recorded wind speeds of three metres per second (= 10.8 kilometres per hour) were rare. Nevertheless the effect of the wind speeds on the catches of the different species of mayflies could be readily observed. As expected, the effect was particularly noticeable during the evening peak, and can be demonstrated on data from both years. In Fig. 49 the data from year II have been employed. The arithmetic mean half catches (see Procedure), per first sampling hour of the night — of various species of mayflies have here been plotted against the wind velocities (in kilometres per hour) experienced during the first sampling hour of the nights. The number of first sampling hours showing the wind velocities indicated in the abscissa, are given in Table VI below.

It is evident from Fig. 49 that the catches of *C. notabile* imagines: (*C.n.*i); *A. ugandanus* imagines and sub-imagines: (*A.u.*i & *A.u.*s-i); *E. bugandensis* imagines and sub-imagines: (*E. b.* i & *E. b.* s-i); *E. curtus* sub-imagines: (*E.c.*s-i); *T. maculatus* sub-imagines: (*T.m.*s-i); and *A. decoratus* imagines and sub-imagines: (*A.d.*i-E & *A.d.*s-i) decrease at high wind velocities (the symbols in brackets are those used in Fig. 49). The same effect of the wind has been found for the other species and stages dealt with, *C. dentatum* included. And the effect applies equally well for the catches in the dawn peak.

It can be shown that small catches of *E. curtus* sub-imagines on windy evenings do not necessarily lead to small catches of *E. curtus* imagines the following morning. This will be gathered from Table VI. In this table, the mean half catches of *E. curtus* sub-imagines per first sampling hour of the night and the arithmetic mean half catches of *E. curtus* imagines taken during the remaining eleven hours of the night, have been shown against the wind velocity prevailing during the first sampling hour of the night.

Table VI. *Catches of E. curtus during year II in relation to wind strength.*

Wind in km/hr. First sampling hour of the night	Number of events	Nightly mean half-catches of *E. curtus:*	
		Sub-imagines, (First hour)	Imagines (Last eleven hours)
0–0.9	85	287.57	84.37
1–1.9	67	302.59	127.98
2–2.9	51	319.26	120.51
3–3.9	37	154.03	93.16
4–4.9	15	54.67	96.86
5–5.9	9	40.56	186.22
6–6.9	2		25.50

I have no information to show that the mayflies become inactive at high wind velocities, and I assume therefore that the decrease in catches at these velocities is mainly due to the wind making it difficult for the insects to enter the trap. Unless combined with violent rain or a drop in temperature, squalls of wind during the night — provided they subside before dawn — seem to have little effect on the catches in the morning peak. The effect of wind during the day on the surviving populations of mayflies cannot be assessed, nor is the effect of the wind on the emerging insects an easy matter to determine. In the latter connection it should be pointed out that as the emergence in the Napoleon Gulf takes place at night, for a lot of species actually in a fixed post-sunset peak, the insects emerge at a time when the wind is normally weak and the water calm.

The mayflies observed to emerge from the Napoleon Gulf, did so after first floating to the surface; the time taken between the insects reaching the surface till they flew away being a matter of seconds. The manner of emergence has been described by SCHOENEMUND (1930). Moderate waves seem unlikely to increase the mortality amongst such emergers. Rainstorms experienced during emergence (or winds strong enough to produce "white horses") are likely to increase the mortality among mayflies emerging from the Gulf. But rain rarely falls during the first hour after sunset — the principal time of emergence — at Jinja; and during year II rain was only experienced to fall during the first hour after sunset on nine evenings out of a total of 266 evenings.

One advantage of flying at night, is that the mayflies are seldom exposed to high wind velocities during the flight activity periods. The flying populations are therefore not much affected by the wind direction.

At Jinja the temperature and the humidity are so closely linked that it is hardly possible to separate the effect of the two factors entirely. It has been mentioned that temperature influences the moulting, and the humidity during the day determines the chances of survival of the population of adults that spends the day quiescent.

As mentioned before, year II was somewhat hotter and drier than year I. In Table VII (page 43) is listed the catch imago ratio (expressed as the percentage of imagines in the total catch) of some species for both years. For *A. decoratus* two sets of ratios have been given: the i.M.- and the i.E.-fractions expressed as the percentage of the total catch. The i.E.-fraction is regarded as being the number of imagines caught during the first sampling hour of the night; the i.M.-fraction is regarded as being the number of imagines caught during the last eleven hours of the night.

For the species in group I, the imago ratios have generally increased from year I to year II. *C. corbeti* females imagines show a small decrease, but this is explained by the fact that a few sub-imagines — absent in the catches from year I — were taken in year II.

For the two species from group III, the imago ratios show an overall decrease from year I to year II. *A. decoratus* behaves contrary to expectation; the i.M.-ratios showing a decrease, and the i.E.-ratios showing an increase from year I to year II. This deviation on the part of *A. decoratus* is not completely understood. It could perhaps be suspected that the species does not belong to group II and that the species has a different flight activity from the one described. This is,

Table VII. *The catch imago ratio for males and females of seven species of East African Ephemeroptera.*

Species	Sex	Stage	Ratios in % of total catch		Increase or decrease in ratio from year I till year II	
			Year I	Year II	Increase	Decrease
Group I:						
E. curtus	m.	i.	23.8	27.6	3.8	
—«—	f.	i.	18.1	18.1		
T. maculatus	m.	i.	12.9	19.4	6.5	
—«—	f.	i.	6.0	6.3	0.3	
C. corbeti	m.	i.	100.0[1]	100.0[1]		
—«—	f.	i.	100.0[1]	99.3		0.7
H. fasciatus	m.	i.	100.0[1]	100.0[1]		
—«—	f.	i.	100.0[1]	100.0[1]		
Group II:						
A. decoratus	m.	i. M.	90.2	84.3		5.9
—«—	f.	i. M.	76.5	72.1		4.4
A. decoratus	m.	i. E.	6.0	9.3	3.3	
—«—	f.	i. E.	6.8	7.6	0.8	
Group III:						
A. ugandanus	m.	i.	83.6	63.3		20.3
—«—	f.	i.	99.1	79.0		2.1
E. bugandensis	m.	i.	12.6	8.6		4.0
—«—	f.	i.	65.2	62.2		3.0

however, very unlikely. Thus to mention one fact, there is no relation between the catches of sub-imagines in the dusk peak and the humidity experienced during the previous day. The same lack of relation is found for the catches of imagines in the dawn peak (i.M.). The relation between the catches of imagines (i.E.) during the dusk peak and the humidity recorded during the day, has already been demonstrated (Table III & IV).

The latter relationship is also shown by the species in group III. This has been demonstrated in Fig. 49, where the arithmetic mean half catches (per night) of *C. notabile*, *E. bugandensis* and *A. ugandanus* (year II) have been

[1] Sub-imagines not caught.

plotted against the humidity recorded at midday. As seen, the mean catches increase from a low to a higher humidity, and decrease as the highest humidities are approached. As mentioned before (page 34) high humidity during the day is indicative of violent rains, which, by killing off parts of the adult population, probably provide part of the explanation for the low catches in evenings following days with a very high humidity. On the other hand, rain during the day will by increasing the humidity, increase the chances of survival for the adult insects that do survive the rain.

The imagines of *E. curtus*, *C. corbeti* and *T. maculatus* caught during the evening peak do not all appear to conform quite to the same pattern as shown by *A. decoratus* and the species in group III above. This can be seen from Table VIII below.

Table VIII. *Arithmetic mean half catches ("first hour" catches per night) of three species of East African mayflies at various midday and sunset humidity ranges in year II. (rH-MD = midday humidity; rH-SS = sunset humidity). The number of events are the same as those shown in Table III and Table IV.*

Humidity range		Arithmetic mean number of individuals caught in a set of two chambers during the first hour of sampling, and the humidity recorded the previous day.					
		E. curtus i.		*C. corbeti* i.		*T. maculatus* i.	
rH—MD	rH—SS	rH—MD	rH—SS	rH—MD	rH—SS	rH—MD	rH—SS
30—39	[1]	3.30	[1]		[1]	0.06	[1]
40—49	40—49	0.20		0.15			
50—59	50—59	0.11	0.06	0.09	0.18	0.01	
60—69	60—69	0.14	0.14	0.07	0.10	0.02	
70—79	70—79	0.06	0.51	0.03	0.09	0.03	0.04
80—89	80—89		0.20				0.02
90—99	90—99						

The mean catches are small, but show a decrease towards the highest humidities. The high mean catches of *E. curtus* imagines for the midday humidity range of thirty to thirty-nine per cent relative humidity stem from one single evening (4th March 1958) when fifty-three imagines were found in the set of two chambers. (This evening catch is by far the highest catch of *E. curtus* taken in any evening peak.) This unique catch cannot at present be satisfactorily explained.

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[1] Humidity range 30—39% rH not experienced.

In Figs. 48—49 the arithmetic mean catches of various species caught (per night) in a set of two chambers are shown against varying temperatures at sunset and at sunrise. The same has been done for varying humidities at sunset. As far as the different temperatures are concerned, the number of evenings and mornings (in year II) when the temperatures were recorded (number of events) are given below:

Temperature	15	16	17	18	19	20	21	22	23	24	25	26
Number of events; sunset					6	9	13	36	72	75	43	12
Number of events; sunrise	2	3	10	46	79	71	34	15	6			

The number of events: humidities at sunset — see Table IV. In the two figures, the species have been indicated by the first letter of the generic and the specific name; the stage has been indicated by i (imagines) or s-i (sub-imagines).

Before discussing the results given in Figs. 48—49, it must be made clear that the temperatures and the humidities recorded at sunset, and the temperatures recorded at sunrise, are not identical with those experienced during the dusk and the dawn activity peaks of the different species. The discrepancy between the sunset temperature (or humidity) and the temperature (or humidity) at the time of the dusk activity peaks is the greater (cf. Fig. 4 for year I).

As evident from Fig. 49, the mean catches of the species active in the dawn peak (*E. curtus* imagines; *A. decoratus* imagines (i.M.); *C. corbeti* imagines, and *H. fasciatus* imagines) increase with higher morning temperatures. Considering the effect of the temperature on the activity and the exuviation, such an increase in the catches is not surprising. In *H. fasciatus* there is a marked rise in the mean catches at the unusual sunrise temperature of twenty-three degrees Celsius. Accordingly, rare as this species is in the catches, we can not as yet entirely discard the possibility that the species shows some flight activity after sunrise on colder mornings. The recorded sunrise humidities (number of events) during year II, were as follows:

rH range (%) at sunrise	50—59	60—69	70—79	80—89	90—99	100
Number of events	2	7	13	69	173	2

Really dry mornings (recorded relative humidity below fifty per cent) were thus not experienced.

It is further evident from Fig. 49 that *E. curtus* sub-imagines; *A. decoratus* sub-imagines & imagines (i.E.), and *T. maculatus* sub-imagines are caught in greater numbers as the sunset temperatures increase from a low to a higher temperature. But for the highest sunset temperatures, the arithmetic mean catches of the three species are reduced. As the highest sunset temperatures are linked with the lowest sunset humidities, it is not possible to tell which of the two factors is the more important in reducing the activity and the catches of the insects (see Fig. 48).

The species in group III present a somewhat different picture and some differences in behaviour are evident between the three species in this group. Mass catches of *C. notabile* tend to occur on cool, calm evenings following rain and a fair day humidity. The same tendency but to a lesser extent is shown by *E. bugandensis* imagines and sub-imagines. A maximum in the arithmetic mean half catches of the two species at a low sunset temperature (and a high sunset humidity) is evident from Fig. 48. In this figure the sub-imagines (of both *E. bugandensis* and *A. ugandanus*) caught during the first sampling hour and those caught during the remaining eleven sampling hours of the night have been indexed (1) and (11) respectively.

It is possible that rain may cause more sub-imagines of *E. bugandensis* to emerge, and that this would to some extent be responsible for the sharp maximum in the arithmetic mean catches at a low sunset temperature. The same may apply to *A. ugandanus* sub-imagines and *C. notabile*. However in the case of the latter, heavy catches would be expected to follow the rain by one or two days — as we are here collecting imagines of a species that is evidently fairly long-lived. But to prove — or disprove — such an effect of the rain, studies would have to be made on the emerging population to avoid the errors involved in the light trap catches.

Considering the maxima in the mean catches of the imagines of the three species mentioned (Fig. 48), the maxima shown at a low sunset temperature (and a high sunset humidity) are probably in the main caused because a high humidity during the day have decreased the mortality rate of the day surviving populations. A second maximum in the catches at a high temperature may be the result of an increase in the intensity of the flight activity of those individuals that have managed to survive the day.

The amount of cloud cover has its effect on the survival, the moulting and the flight activity of mayflies through its effect on temperature, humidity and light intensity. On cloudy days the insolation is reduced, resulting in a moderate temperature and a moderate humidity, increasing the chances of survival for the mayflies that spend the day quiescent. On cloudy nights the loss of heat through radiation is reduced, thus preventing really cold morning temperatures. On dark overcast mornings in year I, morning flying species — not normally represented in the last ten minute sample of the night — were found to be present, though only in very small numbers. The light intensities recorded for these dark mornings were far below normal. It is thus likely that the species active in the morning will prolong their activity provided the morning is very dark and overcast.

Table IX. *The nightly mean half catches of five species of mayflies as related to the rain recorded during the first hour of the sampling night.*

Rain in inches: first hour	Number of events	*T. maculatus*		*E. curtus*		*A. decoratus*		*C. corbeti*		*C. notabile*
		s.-i.	i. M.	s.-i.	i. M.	s.-i.	i. M.	s.-i.	i. M.	i. E.
0.00	257	8.31	1.28	335.03	108.92	9.01	71.44	0.01	5.93	206.60
0.01	2	14.00	0.50	119.00	22.50	3.00	25.00		2.50	62.50
0.02	2	18.00	2.00	89.50	32.00		2.00		0.50	5.50
0.03	1	3.00	1.00	104.00	278.00	9.00	39.00		15.00	319.00
0.04	1				4.00		2.00		1.00	48.00
0.07	1		1.00	318.00	136.00	16.00	7.00			
0.08	1			1.00	1.00		8.00			
0.48	1						1.00			3.00

s.-i. = sub-imagines total; i. M. = imagines taken during the last eleven hours of the night; i. E. = imagines taken during the first hour of the night.

In Table X, the arithmetic mean half catches of five species of mayflies have been shown in relation to the rain recorded for the last eleven sampling hours of the nights.

Table X. *The nightly mean half catches of five species of mayflies as related to the rain recorded during the last eleven sampling hours of the night.*

Rain in inches: last 11 hours	Number of events	*T. maculatus*		*E. curtus*		*A. decoratus*		*C. corbeti*		*H. fasciatus*
		s.-i.	i. M.	s.-i.	i. M.	s.-i.	i. M.	s.-i.	i. M.	i. M.
0.00–0.09	216	8.33	1.46	339.15	117.01	8.61	78.23	0.01	6.54	1.32
0.10–0.19	10	8.60	0.90	353.50	105.10	15.20	49.10		2.50	0.70
0.20–0.29	6	13.33	0.50	496.17	147.50	6.16	42.67		6.83	1.17
0.30–0.39	10	5.40	0.40	129.80	44.60	6.80	22.40	0.10	2.40	0.30
0.40–0.49	8	9.39	0.50	148.88	31.26	7.63	15.38		1.76	0.38
0.50–0.59	2	4.50	0.50	135.00	20.50	0.50	4.50		2.50	
0.60–0.69	4	4.75	0.25	375.25	97.00	13.00	58.25		4.50	
0.80–0.89	2	18.50		140.00	10.50	7.00	14.00			
1.00–1.09	1	8.00		354.00	6.00	3.00	9.00			1.00
1.10–1.19	2	7.50		515.50	21.50	13.00	15.00			
1.20–1.29	2	3.00		292.00	22.00	8.50	25.00		2.50	
1.40–1.49	1	6.00		247.00	64.00	12.00	86.00		1.00	
1.60–1.69	1	7.00		309.00	7.00	40.00	26.00			
2.10–2.19	1	1.00		119.00	1.00	4.00	8.00			1.00

s.-i. = sub-imagines total; i. M. = imagines taken during the last eleven hours of the night.

Some of the probable effects of rain on the populations and catches of mayflies have already been mentioned and will not be repeated here. Slight rain during the dusk or dawn peaks did not seem to affect the catches. But with increasing intensities of rain, the catches of mayflies diminished. This, no doubt, was partly caused by an increase in the wind velocities and a drop in temperature that tend to follow moderate to heavy rains. But apart from that, is seems likely that the rain has in itself caused some damage to the flying populations of mayflies. In Table IX the arithmetic mean half catches of five species of mayflies are seen in relation to the rain recorded during the first sampling hour on the 266 sampling nights in year II.

It is seen from Table IX and Table X that the numbers of nights when much rain has fallen during the first hour or during the last eleven hours are very small. But it is nevertheless evident that 1) moderate to strong rain during the first hour of the night leads to a decrease in the numbers of sub-imagines caught and — what is quite important — a decrease in the numbers of imagines (i.M.) caught in the morning; 2) moderate to strong rain during the last eleven hours of the night usually leads to small catches of imagines (i.M.) during the last eleven hours of the night. Species from group I have been used to demonstrate this.

Moderate to heavy rain experienced during the night when the sub-imagines have settled down to moult, reduces the catches of imagines (i.M.) in the morning peak, and it probably reduces the catches partly by damaging the moulting insects. Moderate to strong rain during the dawn peak also reduces the catches of mayflies, in the same way as rain during the dusk peak reduces the catches of insects during the evening peak. It should not be forgotten that rain during the last eleven hours of the night also tends to affect the temperature, the humidity and the wind velocity, factors that have an important bearing on the catches of mayflies, as well as on the populations and their activity.

The flight activity of the mayflies dealt with in the present communication, takes place at times when the conditions of temperature, humidity and wind are normally very favourable. But the diel flight activity patterns are, as we have seen, rigidly rhythmic in nature. None of the three climatic factors mentioned above show such a rhythmic pattern, and the same holds good for rain fall and cloud cover. Accordingly, none of the climatic factors mentioned can explain the rhythmic patterns of the mayflies. (It could perhaps be suspected that the fall in temperature (and rise in humidity) taking place in the evening after sunset could be the governing factor (factors) for the rhythmic flight activity of the species in group III. But this could not be so. The fall of the temperature might take place at varying times after sunset, without a similar variation in the flight activity of the species being noticed. And the fall of the temperature could not be the only factor operating, as falls of temperature are readily experienced during the day without any notice having been made of flight activities in the species concerned. The theory also fails badly in explaining the dawn peaks — small as they are — in *A. ugandanus* and *C. notabile.*)

HADDOW (1954) studying the biting activity of mosquitoes found (*loc. cit.* p. 233): "With reference to possible release mechanisms, the most important microclimatic factor must almost certainly be light. Thus a large number of species cease biting at sunset, while others begin to bite at this time, and much the same is true of sunrise. The speed with which many of these changes of behaviour occur is such that it can be attributed only to the rapid light changes of these periods in the tropics. No other factor changes with sufficient suddenness to explain the facts.".

As noticed from Fig. 22, the flight activity peaks of most species of mayflies are closely related to sunset and sunrise. Presuming that the flight activity pattern is brought about — partly or wholly — by extrinsic factors, light must be the most important one. But the occurrence of intrinsic rhythms — a "physiological clock" (cf. BÜNNING, 1958) — cannot be ignored. We are left then with the following preliminary conclusion, that the flight activity patterns could be explained by the extrinsic factor: light, and/or by an intrinsic rhythm. If the activity pattern is in part extrinsic, and in part intrinsic, we would be dealing with a composite activity pattern, (cf. ALLEE, EMERSON, PARK, PARK, & SCHMIDT; 1949). Field studies lend themselves poorly to studies of the true nature of the activity rhythms encountered (HARKER, 1958), but the problem will be further discussed in the following chapter.

Discussion

In temperate regions, the emergence, moulting and flight activity of mayflies present a varied picture. It is therefore dangerous to generalize. The adults of mayflies are short-lived and vulnerable insects, and there is a definite need for synchronization in the activity of the two sexes in order to ensure fertilization of the females. Synchronization is to a large extent brought about by a strictly seasonal emergence of adults; the seasonal emergence being the common denominator for all species of mayflies in temperate regions. Mayflies vary from sp. to sp. with regard to the time of their emergence in the diel cycle (NEEDHAM, TRAVER & HSU, 1935), but it often takes place by day. The duration of the diel emergence period varies with the species (BERNER, 1950). As the time of emergence varies from species to species, it is not surprising that various authors (cf. RAWLINSON, 1939) have related the phenomenon of emergence to various external factors. Factors like temperature, wind and rain (not to mention air humidity) cannot explain all the cases of rhythmic emergence in the *Ephemeroptera*. Indeed NEEDHAM (1920) found no correlation between climatic factors and the emergence of *Hexagenia bilineata* (SAY). It is understandable that the relation between light and emergence has attracted interest (cf. EDMUNDS, 1948). Moulting by day appears to be quite usual in temperate regions. The species that emerge in spring — or else are found at a high altitude or at a high latitude are often diurnal in their flight activity habits. In the species that emerge later in the year — or else are found at a low altitude or a low latitude — the tendency towards nocturnalism is stronger. It is known that the same species may have different times of eclosion and flight activity at different localities (VERRIER, 1956). In temperate regions the flight activity of mayflies is very dependent on climatic factors such as temperature and humidity (VERRIER, 1956; COOKE, 1942, 1947, 1952).

The picture presented by the mayflies studied at Jinja, is somewhat different. The species do not show a seasonal emergence. *P. adusta* shows a lunar periodicity of emergence in Lake Victoria (HARTLAND-ROWE, 1955), the synchronization of adult activity being here both a lunar and a diel one. And it has been suggested (CORBET, 1957) that (*loc. cit.* p. 250): "It may be that *P. adusta* exists at too low a density for continuous emergence to be practicable from a reproductive point of view. Although dense masses of adults are encountered around lights on swarm nights, the nightly numbers would be small were these adults to be distributed evenly throughout a month.". In the remaining species mating is ensured by an effective diel synchronization of the population activity alone, achieved through a synchronization (and co-ordination) in the diel emergence, moulting and flight activity.

The flight activity of the mayflies at Jinja is almost exclusively nocturnal, as is the emergence — where known. Both activities are rhythmic and the only extrinsic factor that could bring about such rhythmic phenomena would be light. Whatever the true nature of these rhythms, it is tempting to consider them as having resulted from evolutionary processes whereby the selective action of physical factors (particularly air humidity and wind velocity) and biotic factors has been working according to the rule of natural selection. These problems will be discussed in more details later.

In the mayflies studied, the sub-imaginal flight activity seems to follow immediately on emergence, there being no evidence to show that one emergence group flies more than once as sub-imagines. The flight activity histograms (Figs. 13a & b, 14a & b, 15a & b, 16a & b, 17) and observations in nature show that emergence and the subsequent sub-imaginal flight activity are unimodal and are related to the time of sunset and sunrise. *T. tinctus* is exceptional in this respect; from certain other species the sub-imagines were not recorded. There is at Jinja a definite post-sunset emergence peak, which can be readily observed, during which large numbers of mayflies and caddis-flies emerge. Some mayflies emerge later at night (*T. tinctus* females); a few emerge shortly before sunrise (some *Caenidae*).

It is not possible from the present study to tell how, when and at what stage (or stages) in the pre-sub-imaginal development the synchronization in emergence is achieved. The close relationship between the times of sunset and the times of emergence may mean that the emergence is triggered off by the rapid decrease in light intensities at and after sunset. In the case of the *Caenidae* mentioned, the rapid change in the light at dawn may possibly be responsible for the pre-sunrise emergence peak encountered here. The explanation may not, however, be so simple. A few short references to some recent studies, will demonstrate this.

HARKER (1953) studying three species of British mayflies, showed that the larval activity pattern was laid down in the egg or during the early larval life by the daylight cycle. The activity pattern of larvae taken from a natural habitat persisted under continuous light or darkness. By rearing larvae from the egg in constant light, she also showed that arrhythmic larvae could be produced. Such larvae, when subjected to a short abnormal period of darkness, picked up a corresponding abnormal activity rhythm.

It is reasonable to assume that there is a relation between larval activity and emergence. HARTLAND-ROWE (1958) considers the lunar periodicity of emergence of *P. adusta* to have been induced in the larvae by variations in the light intensity of the moon. He suggests that the lunar rhythm may be laid down early in the larval life, but the evidence for this is slight, and he does not exclude the possibility that (*loc. cit.* p. 195): "— — -- a series of stimuli at regular intervals might induce a rhythm in the larvae, this rhythm being translated into an emergence rhythm at maturity.". FRYER (1959) favours a different explanation.

The problem concerning the ways in which diel rhythms are induced in the animal kingdom is a complex one and has attracted much interest lately (cf. HARKER, 1958). Studies by PITTENDRIGH (1954) and PALMÉN (1955, 1956, 1958), though concerned with certain *Diptera*, are of special interest in the present connection.

PITTENDRIGH (1954) studied emergence in a strain of *Drosophila pseudoobscura* STURTEVANT which emerges during the early hours of daylight. He showed that the periodicity of emergence persisted in continuous darkness if — at some developmental stage other than the prelarval — the insects had been subjected to a diel change in illumination. The reference point for timing the almost simultaneous emergence was shown to be the darkness to light transition (*i. e.* dawn). An arrhythmic emergence activity resulted if the cultures were reared and permanently kept in total darkness. If such arrhythmic larvae were subjected to a single light shock, they (*loc. cit.* p. 1021): "— — —, immediately start measuring off such intervals following experience of a single *unrepeated* event corresponding with the reference point for the cycle in nature.". He also showed that once a rhythm had been induced, it could be inverted or reset merely by introducing a new darkness to light transition (another "dawn") different in time from the one the culture had been set to previously.

PALMÉN (1955, 1956, 1958) studied the rhythmic emergence in *Chironomidae* and the results obtained indicate the occurrence of an endogenous "clock" in species of this family. The bursts of emergence in the species studied by him were fixed in relation to the day-to-night transition of the diel cycle. In *Allochironomus crassiforceps* KIEFF. the normal emergence rhythm was maintained in a population of larvae (previously exposed to normal photoperiods) even though the population was kept in constant darkness for six days. PALMÉN (1958) concludes that (*loc. cit.* p. 819): "— — —, as in *Drosophila* (PITTENDRIGH, 1954; BRETT, 1955) for instance, the "internal clock mechanism", once set in motion, cannot be altered by means of excluding the light, at least not when the individuals of *A. crassiforceps* are either full-grown larvae ready to pupate, or pupae ready to emerge. In this case, an adaptation to the normal photoperiod must already have occurred at an earlier stage of development. It still remains unknown to what extent periodicities other than the usual 24-hour one can be induced at earlier stages of development.".

Our knowledge of the larval activity patterns in *Ephemeroptera* is not profound, and our knowledge of the nature of the known activity rhythms is small. As the existence of an "internal clock mechanism" determining the larval activity pattern has recently been found in the order (HARKER, 1953), the possibility cannot be excluded that the synchronized emergence of mayflies at Jinja may in some, if not in all, species have been brought about at least partly by the action of an endogenous "clock". It does not seem altogether unlikely that a stimulus (or a series of repeated stimuli) given by dusk or dawn, both so marked in the tropics, may induce a persistent rhythm in the larvae. Such an activity rhythm could then be translated into an emergence rhythm at maturity, as suggested by HARTLAND-ROWE (1958), and could perhaps even persist during the short adult life in some species. Since the day and the night are of approximately the same duration, the larvae could theoretically use either dusk or dawn as a time reference point.

In *P. adusta* the flight activity pattern is solely a function of the emergence period. The flight activity period of this species tells us little apart from the fact that the flight activity is not inhibited within this period. The same seems true for the females of *T. tinctus*. Regarding the relationship between emergence period and flight activity, some *Caenidae* met with at Jinja are not dissimilar to *P. adusta*. *P. adusta* does not alight to moult, the *Caenidae* in question do, but they alight for a couple of minutes only, resuming their flight as soon as the moulting is completed. With the possible exceptions of the lowest temperatures, the morning temperatures experienced at Jinja are not likely to alter the duration of the moulting process in the *Caenidae* sufficiently to make a comparison with *P. adusta* invalid on this score. The males of *T. tinctus* take some more time to moult, but even they take off without any significant delay once the moulting is completed. The delay in exuviation is such that the male imagines are about when the females appear, thus securing a close synchronization between the flight activity of the two sexes. *T. tinctus* seems to be the only species (of those in which sub-imagines were recorded) where one sex emerges considerably later than the other in the diel cycle. A similar phenomenon is well known in other mayflies elsewhere (cf. Edmunds, Nielsen & Larsen, 1956; Schoenemund, 1930). The fact that males and females emerge almost simultaneously in the diel cycle, does not exclude the possibility that, within one generation of mayflies, the emergence of the males may precede that of the females by one or more days. There is little evidence of this in my data, but such a phenomenon could be masked. It is not unusual in larvo-aquatic insects that the males develop more rapidly than the females (cf. Penn, 1947; Qutubuddin, 1953; Nielsen & Haeger, 1954; Nielsen & Greve, 1951).

In several species there is a considerable delay between the completion of ecdysis and the imaginal flight. These species are all crepuscular. In some of them it seems that not only crepuscular light intensities, but also the nature of the light experienced at dusk and dawn, stimulate flight activity at these periods. But let us first consider the delay of the imaginal flight.

In *E. bugandensis* and *A. ugandanus* the exuviation takes place after sunrise on the day following emergence, and as the insects are flight inhibited during the day, the imaginal flight cannot take place until approximately twenty-four hours after emergence. In *T. maculatus*, *A. decoratus* and *E. curtus* (and probably also in *C. corbeti* and *H. fasciatus*) ecdysis takes place during the night — less than twelve hours after emergence. For *E. curtus* at least there is evidence which indicates that moulting is accomplished more rapidly on warm than on cold nights. This was of course to be expected, and probably applies to the other species as well. It has been demonstrated in various species of mayflies by Clemens (1917), Traver (1931), Crass (1947) and Lyman (1944a). Working on the teneral development and behaviour in *Aphis fabae* Scop. (*Hemiptera*), Taylor (1957) who defined the teneral stage as (*loc. cit.* p. 207): "— — — the interval between eclosion of the alate imago and flight when flight is not extrinsically activated or inhibited.", found that the duration of the teneral period depended on the temperature, but that the temperature changes per se, or other climatic factors, had little effect on the rate of development during the teneral period. He also found that behaviour, operating as an inhibitor of flight, added to the teneral time. *Aphis fabae* is diurnal. The daily flight activity pattern is somewhat variable, but is often bimodal (JOHNSON, TAYLOR & HAINE, 1957); it being mentioned by JOHNSON & TAYLOR (1957) that (*loc. cit.* p. 209): "— — —, on different days the two peaks may differ widely in relative height, amplitude and time of occurrence; one may be suppressed or merged into the other. Such variations depend on the temperature and on the organisms' relations to it; — — —". In the mayfly *E. curtus* however, although the arrival of the first newly "hatched" imago in the trap occurs earlier on warm than on cool nights and notwithstanding the fact that the gradual build up towards the morning peak is more protracted on these nights, the peak catches occur at a time related to the times of sunset and sunrise. We must indeed assume that *T. maculatus*, *A. decoratus*, *C. corbeti* and *H. fasciatus* also moult earlier on warm than on cool nights. But even here, the peak catches occurred at a time related to the times of sunset and sunrise; though a morning peak was absent in some species when the morning temperature was low.

The peak catches of the different imagines occurred as follows. In the evening, peak catches of *E. bugandensis*, *A. ugandanus* (i. E.), *A. decoratus* (i. E.) and *C. notabile* were experienced from the end of the civil twilight till the end of the nautical twilight. In the morning, peak catches of *A. ugandanus* (i. M.[1]), *A. decoratus* (i. M.), *E. curtus*, *H. fasciatus*, *C. corbeti* and *T. maculatus* have been taken in the corresponding twilight period. The last species also shows a peak near the beginning of the astronomical twilight in the morning, but this peak may be accidental. The peak catches of *C. notabile* in the morning have been experienced near the beginning of the civil twilight (*i. e.:* the sun approximately six degrees below the horizon). For reasons given previously (see page 24) the ten minute sampling period yielding the peak catches may not be strictly indicative of the ten minute period showing the maximum flight intensity, but the time of occurrence of the peak catches proves that the species concerned have their flight activity maximum within the evening and morning twilight; thus that the species are crepuscular in their flight activity habits. If the Figs. 9, 10, 12, 13a & b, 14a & b, 15a & b, 16a & b, 17 and 22 are consulted, it becomes evident that the flight activity is not for all the crepuscular species strictly limited to the twilight hours. Some flight activity takes place during the rest of the night.

The flight activity shown by the crepuscular species outside the twilight hours — though seemingly unimportant — is of some interest. CORBET &

TJØNNELAND (1955) suggested for some crepuscular East African *Trichoptera*, that flight activity was strongly stimulated by certain crepuscular light intensities, and they suggested that the overall activity might well be greater on moonlit nights. RIBBANDS (1946) studying the activity of some mosquitoes in West Africa found a positive correlation between the time at which females of *Anopheles funestus* GILES entered huts and the time of moonlight. He also found that flight activity was partially inhibited during moonless periods of the nights, and that the mosquitoes entered the huts in numbers when the moon came out. On nights with no moon, the mosquitoes waited until twilight the following evening before entering. In the case of the crepuscular mayflies, there seems to be no relation between the flight activity experienced outside the twilight hours and the "crepuscular" light intensities provided by the moon. Neither do "false dawns" nor "false dusks", provided by the moon when it sets or rises in the dark period of the night, have any noticeable effect on activity. (The argument that such an aberrant flight activity could have been produced but failed to be expressed in the catches from moonlit periods (cf. WILLIAMS, SINGH & EL ZIADY, 1956), appears irrelevant, as it does not afford a satisfactory explanation as to why no trace is found of such an activity. The crepuscular mayflies were normally caught at times during dusk and dawn when the light intensities were equal to, or exceeded those of, full moon. Moreover the twilight flight activity patterns remained the same irrespective of the phase and the light intensity of the moon.)

How is then the crepuscular flight activity of the imagines brought about?

Of the species mentioned above, *E. bugandensis* is the only one that does not show a peak catch, however small, at dawn. The reason could simply be that the imagines do not live to fly in the morning in nature, though as far as the longevity experiments can be relied on, the insects may be capable of surviving that long. If the latter assumption is correct, the question remains if the lack of catches is an effect of the low temperatures prevailing in the morning. Apart from the effect of low temperatures on moulting and flight activity (LYMAN, 1944b; COOKE, 1947), they may also cause a change in the phototropism of mayflies (cf. ALLEE & STEIN, 1918; BERNER, 1950). None of these explanations can however apply, as catches of *E. bugandensis* imagines have been taken at dusk at temperatures comparable to some of those recorded in the morning (cf. Figs. 48—49). It should also be mentioned that KENNEDY (1925) reports that *Ephemera guttulata* PICTET changes its phototropic response, becoming negatively phototropic after copulation. Even if applicable to *E. bugandensis*, this would fail to explain why males have not been taken in the dawn peaks.

In principle the flight activity pattern of *E. bugandensis* imagines could be explained as a release from flight inhibition once the influence of daylight is removed at sunset; the release into activity being followed by a declining curve of exhaustion. In principle, this hypothesis was advanced by LUMSDEN (1952, 1957) to explain the biting activity of certain mosquitoes. Too close a comparison between the biting activity of mosquitoes and the flight activity of insects cannot be undertaken for reasons given by CORBET & TJØNNELAND (1955).

The hypothesis is clearly less successful in explaining the flight activity pattern of the imagines belonging to the other crepuscular species. Nor can the hypothesis launched by CORBET & TJØNNELAND (1955) as it stands (see page 55) fully explain the flight activity pattern encountered, as there is no apparent connection between moonlight and flight activity. The reason for the lack of relation cannot be that flight activity can only be induced by crepuscular light intensities exceeding those of full moon, as this would fail to explain the early beginning of the dawn activity peak. Unless the insects have an intrinsic flight activity rhythm coinciding with the times of dusk and dawn — which seems somewhat unlikely — we are led to believe that not only low light intensities as such, but also the quality of light is important in inducing the flight activity in crepuscular mayflies.

When discussing the biting activity of some mosquitoes showing more than one biting activity peak per night, LUMSDEN (1952) suggested that different age groups might bite at different times, and (*loc. cit.* p. 779): "— — —, in the case of nocturnally active mosquitos, the first wave of activity after sunset might be mainly composed of older mosquitos, while those attacking later in the night might be mainly newly-hatched females whose advent had been delayed by some other activity, such as mating.". This hypothesis appears to have gained little support from other workers studying the biting activities of mosquitoes (SENIOR WHITE, 1953; HADDOW, 1954; GILLIES, 1957b). But in *Simulidae*, DAVIES (1955), using the change of the fat-body as an indicator of age, has showed that the population of *Simulium ornatum* MG. biting in the evening was composed of older females than those biting by day. Reviewing recent works on the biting activity of mosquitoes, LUMSDEN (1957) has discussed his hypothesis at some length. Regarding the diel flight activity peaks shown by some mayflies, the peaks appear largely to be made up of individuals belonging to different age groups (age here reckoned from emergence). This is not surprising considering the short adult life of these insects, and the fact that the adults undergo an ecdysis.

There is a small time lag between the time of the imaginal peak catch at dusk and the time of the peak catch of sub-imagines in *A. ugandanus*, *A. de-*

coratus and *E. bugandensis*. It is worthy of notice that this time lag might have escaped notice had sampling periods lasting notably longer than ten minutes been employed. Though the two peaks are distinct, there is a certain amount of overlapping with regard to the times of flight of the two succeeding emergence populations flying on the same evening. A similar overlap of the flight activity of two, or more, emergence groups is not unusual in *Ephemeroptera*, and the question has been raised whether the male imagines do mate with the female sub-imagines of the succeeding diel emergence group (cf. IDE, 1930; SPIETH, 1940). For the non-parthenogenetic nocturnal species, the behaviour of nocturnal species is of course difficult to observe in nature, breeding experiments on ova from females isolated as sub-imagines should here provide the answers.

PARK (1940) has discussed nocturnalism *versus* diurnalism, and stressed the adaptive value of nocturnalism.

For the adult mayflies concerned, the advantages of nocturnalism are evident. These advantages are especially noticeable when the effects of the two climatic factors: wind velocity and air humidity are considered. Exceptional nights and the rather common post-midnight wind squalls apart, less wind is experienced during the night than during the day at Jinja. Rough waters would seem to cause heavier losses in the emerging populations than would calm waters (PALMÉN, 1955); and calm waters could therefore act as one of the selective factors favouring those species (or mutations) that emerge and fly during the night. Wind has also a pronounced effect on the flying mayflies. A moderate to strong wind will thus carry the swarming mayflies away. In doing so, the sub-imagines may be carried far away from the water, or, what will also cause losses in species where the sub-imagines alight in order to moult: out over the open lake. In general it would appear that the short activity period of the sub-imagines would help to reduce losses in the potential breeding population and facilitate the establishment of a high local concentration of imagines once moulting is accomplished. This concentration effect is made the more effective by a striking synchronization in the flight activity of the imaginal population, the flight activity periods being, as seen, of a limited duration. A reduced vagility is the price paid for such a synchronization. A strong to moderate wind experienced during the mating flights of the species would probably result in few females being fertilized.

Although experiments on the rate of evaporation at various air humidities were not carried out in the mayflies studied, there can be no doubt that the mayflies would be particularly susceptible to desiccation at low air humidities were it generally the rule for the insects to fly during the day in the tropics. They could of course fly immediately after sunrise when the humidity is still high, and some do (cf. *C. dentatum*). It is suggestive that collections of mayflies observed to fly later in the day have yielded sub-imagines only. NEEDHAM, TRAVER & HSU (1935) find it likely that the rate of water lost through evaporation is higher in the imagines (*loc. cit.* p. 100): "Doubtless the removal of the hardened outer cuticle facilitates loss of water by evaporation.".

At all events, by emerging after sunset, the sub-imagines enter an environment where the humidity is fairly high and where the loss of water must be small. My results indicate that moulting generally takes place during the night or very shortly after sunrise, which must be an advantage to the species. But whether most of the species present (but not studied) at Jinja conform to this pattern, remains to be seen. *A. ugandanus*, a successful species here, moults much later in the day.

Rain may not always be advantageous to adult mayflies, as heavy rain will bring about casualties. Harm done by heavy rain would be the more noticeable as the rain tends to fall between sunset and sunrise. But should rainy nights (experienced mainly during the rainy seasons) or cold mornings (occurring occasionally in the dry seasons) prevent diel populations of mayflies from breeding, the natural variation inherent in the growth and development processes in the larvae recruited from other diel breeding populations will fill the gaps in the emergence populations — gaps that might otherwise theoretically have ensued. The disadvantages caused by heavy rain or occasional low morning temperatures are therefore minimised.

As the flight *cum* feeding activity of bats appeared to coincide with the dusk and dawn flight activity peaks of the larvo-aquatic insects, it seems probable that the bats take their toll of the nocturnal mayflies. Other insectivorous animals are active as well. Thus the time from sunset till sunrise is by no means a period free of predators, though the predation pressure may well be less than it would have been, were the flight of the mayflies to have taken place during the day.

As we have already seen, several species of mayflies at Jinja spend the whole, or the important part of (*i. e.* up to and including the reproductive phase) their adult life in the humid atmosphere of the night, though in some, stragglers — mainly males — survive the following day to fly the following evening. Other species must survive a day before being able to reproduce themselves. The species do not show any seasonal emergence at Jinja. Emerging mayflies are therefore available all the year round for the fishes that feed on them, though the size of the emerging populations may vary. In the case of the species that must survive a day as adults, a decrease in the catches of imagines is evident on evenings following days with a low air humidity. Hence, there is a tendency towards a decrease in the catches of imagines in the dry season. This tendency is however secondary. But even if our concept of the seasonal variation in abundance of the various mayflies at Jinja were to be based on the variation in the catches of imagines alone, we would still be unjustified in speaking of a seasonal emergence.

It follows from what has been stated, that the catches of imagines of the day-surviving species are generally higher on evenings following days with a fairly high air humidity; in the main probably the result of an increased survival rate. COLLESS (1952, 1956) working in Borneo has suggested that the same sort of thing occurs in certain mosquitoes. Dealing with *Anopheles leucosphyrus leucosphyrus* DÖNITZ, COLLESS (1956) observes (*loc. cit.* p. 121): "The close association between the increase in catch and the onset of heavy rain suggested that the increase was not due to increased breeding, and it seems possible that the population was immediately increased by the favourable effect on adult survival of higher humidities, particularly in day-time resting places. The writer has published evidence suggesting such an effect on the closely related *A. l. balabacensis* (COLLESS, 1952).".

Little factual evidence exists concerning the lack of seasonal emergence in tropical mayflies. SPIETH (1938) who possessed little definite information, stated (*loc. cit.* p. 214) that: "— — —, in the southern part of the United States, the length of the emergence period of the group is much longer. There seems to be no reason why in the tropics and subtropics there should not be some species emerging during each month of the year.". Working in Florida, the greater part of which cannot be considered sub-tropical (BERNER, 1950), BERNER (1950) confirmed SPIETH's (1938) view. BERNER (1950) reports (*loc. cit.* p. 23): "There are very few Florida mayflies which are definitely seasonal and these few are probably Southern in origin, whereas those species emerging throughout the year are Northern forms which have immigrated to Florida.". And further (*loc. cit.* p. 23): "The generalization that species of Northern origin are nonseasonal in Florida, and that seasonal forms in this state are all of Southern origin, holds good, but this is not a complete statement of the facts. Many of the species believed to be Southern in origin are nonseasonal like the Northern forms in this area.". To study the problem of a seasonal — or a continuous — emergence in tropical mayflies from casual collections alone (cf. ULMER, 1939; SPIETH 1943) is hardly worth while as it is unlikely to lead to any definite conclusions. To be of any help in this respect, such collections would have to be carried out in the same locality at regular intervals throughout the year. And if based on flying mayflies, the diel sample must be extensive enough to cover the diel flight activity periods of the species studied. It is highly likely that one will find that most — if not all — mayflies show a continuous emergence in the majority of tropical localities.

As a group, the *Ephemeroptera* at Jinja exhibits a bimodal flight activity with peaks at dusk and dawn. A similar group activity has been described for the *Trichoptera*, and most of the practical implications mentioned in this connection, apply equally well to the mayflies (see CORBET & TJØNNELAND, 1955). *T. tinctus* is here a rather special case, as the main flight activity takes place outside the twilight hours, an important exception as this species is one of the worst insect nuisances at the Owen Falls Power Station.

The flight activity patterns presented in this paper may be of some interest to collectors of mayflies in the tropics. When it comes to collecting mayflies in tropical localities with a climate similar to that of Jinja (*i. e.* with warm to fairly warm mornings), collecting by light at night will probably be found useful. This collecting, which should preferably take place as near the shores or banks as possible, should be carried out throughout the whole night. If the collecting is restricted to the evening only, the indications are that some species may not be caught at all, some species will be caught as sub-imagines with only a few male imagines thrown in, whereas some species will be adequately represented both with regard to sex and stages. It is probably correct to say that a few whole night samples will prove more representative than a protracted series of evening samples. If whole night catches cannot be carried out, dusk and dawn sampling are likely to give the best results. Several taxonomic papers on tropical mayflies give the method and time of catch as "insects taken at light at night". It would here have been useful if the times of night, when the different stages of the mayflies had been taken, had been stated.

It would be interesting to see the geographic distribution of the various species dealt with in the present communication in relation to their flight activity — the flight activity patterns may incidentally vary somewhat from one locality to the next. A discussion on distribution and flight activity cannot be embarked on as yet, as our knowledge of the geographic distribution of the different species is very incomplete. We do know that *P. adusta* has a wide distribution in Africa; evidently this species only shows a lunar periodicity of emergence in Lake Victoria (HARTLAND-ROWE, 1958). Of the other species, *T. maculatus* is known from Nyasaland (KIMMINS, 1948, 1955) and *E. bugandensis* is known from Tanganyika (Pangani River), where it has been taken by GILLIES (1957a).

It would now be interesting to see what happens to the mayfly fauna and to the mayfly flight activity in "cold-mornings" tropical localities (*i. e.* localities in drier parts and localities at higher altitudes). It is difficult to see how a bimodal dusk-and-dawn flight activity pattern could be maintained here, unless the dawn flight is delayed till after sunrise. Or are any species from the drier parts of Africa able to survive the day to fly the following evening? Or is the mayfly fauna of the lakes in the drier parts recruited from those species that complete their adult life in a couple of hours? (To my knowledge only *Caenis* sp. is known from Lake Rudolf (BUXTON, 1937) at present. More extensive collection from this area would be of interest.) These are some of the questions the present paper leaves unanswered. It is my hope in the future to probe into some of the relevant problems related to the adult biology of *Ephemeroptera.*

Summary

Certain aspects of the adult biology, including the flight activity, of certain East African mayflies have been studied for a period of about two years at Jinja, Uganda.

The mayflies at Jinja are almost exclusively nocturnal in their flight activity habits. Eleven positively phototropic species were chosen for the present study and a Robinson mercury vapour light trap (design no. 862769) was employed in obtaining samples. On all sampling nights, the trap was run from sunset till sunrise.

During the first year, the trap was run once a week, and the trap was emptied every tenth minute throughout the sampling night. Catches obtained in successive ten minute periods were regarded as being an approximate measure of the flight activity throughout the night.

During the second year, the trap was run every night for nine synodic months. The trap was then only emptied twice a night: one hour after sunset and at sunrise. A method for sub-sampling the catch was discovered, whereby the work involved in sorting the catch and identifying the mayflies dealt with, was reduced by a half.

Records were kept of various climatic and external factors, and the flight activity of the mayflies has been studied in relation to these factors. An elaborate statistical treatment of the data collected is not considered admissible. Instead it is inferred that a study of the flight activity of mayflies by means of a light trap, is more a study of consistency of tendencies apparent from the samples taken, than a study of the actual number of insects caught by the trap.

Where studied, the emergence has been rhythmic and — excepting *T. tinctus* — unimodal. In *T. tinctus* it has been suggested that the males and the females emerge at a different time of the evening. Several species of mayflies emerge in the post-sunset emergence peak. This probably applies to most species of mayflies (and caddis-flies) encountered at Jinja. But some mayflies belonging to the *Caenidae* show a pre-sunrise emergence peak. *P. adusta* emerges at the end of the post-sunset emergence period. The lunar periodicity of emergence from Lake Victoria has been confirmed for the latter species.

The emergence was not seasonal in any of the species of mayflies studied.

The flight activity of the sub-imagines is unimodal and of short duration (exception: *T. tinctus*). But the duration of the sub-imaginal stage varies with

the species, and in some (*E. bugandensis* and *A. ugandanus*) it lasts for twelve hours or more. Exuviation takes place during the night or during the early morning in several species, but *A. ugandanus* moults quite successfully later in the day. If the sub-imaginal females of *T. tinctus* moult at all, the moulting is only partial. In a few species (*i.e. P. adusta, T. tinctus* males, and some mayflies belonging to the *Caenidae*) the sub-imaginal period is of a very short duration and there is no delay between exuviation and the subsequent imaginal flight activity (*i.e.* the mating flight). These short lived adults certainly do not live for more than a few hours only, the imaginal flight activity is principally determined by the time of emergence, and basically governed by the factor (factors) governing emergence. The factors governing emergence are discussed. It has been suggested that light and/or intrinsic factors are responsible.

In several species there is a noticeable delay between ecdysis and the subsequent imaginal flight activity. These species show a crepuscular flight activity, as do the bulk of the *Ephemeroptera* found at Jinja. Some of the species fly as imagines in the dawn peak, others fly as imagines in the dusk peak twenty-four hours after emergence. The latter species spend the day quiescent, as they are flight inhibited during the day.

External factors, like temperature, air humidity, wind strength, wind direction, rainfall, the extent to which the sky was covered by clouds, the phase of the moon and the intensities of moonlight cannot explain the crepuscular flight activity patterns found, as they are all of a perfect rhythmic nature; but the effect of the different factors have been discussed. It has been found that some of the factors (wind, rain, temperature and air humidity) play a great part in determining the size of the peaks, and may at times totally suppress them. These factors do not create any new and different flight activity pattern. Their influence is therefore mainly of a repressive nature.

Theories have been suggested to explain the crepuscular activity patterns observed in the imagines concerned. For the bimodal and crepuscular species, it has been suggested that flight is strongly stimulated by light of a crepuscular intensity and a twilight nature. In another species (*E. bugandensis*), flying at dusk only, the flight activity pattern could be explained as a release into activity once the influence of the daylight is removed at sunset (cf. LUMSDEN, 1952).

The adaptive value of nocturnalism in tropical mayflies has been emphasized.

Some practical implications of the present work are briefly mentioned.

Further studies on the flight activity and the geographical distribution of tropical mayflies, as well as general physiological and ecological studies of tropical mayflies, are bound to give valuable results and are very much needed.

Appendix 1.

Data on the sub-sampling method employed during year II (see also page 13 and Fig. 3). The trap was run for a short period after sunset on six different evenings (I—VI). Typical "morning" species are therefore not represented in Table XI below. It is reasonably assumed that the catches of the "morning" species are distributed in the two sets of chambers as are the catches of the species shown in Table XI. Visual inspection was carried out as a check on this point.

In each of the six columns in Table XI, the number of insects found in a chamber set (1 and 3) is mentioned first. The chi-square values, worked out from an expected equal distribution (50%—50%) of insects in the two sets of chambers, have been cursivated. Though the numbers caught were at times small, I have not used the formula for adjusted chi-square below (cf. SNEDECOR, 1953). The chi-square was not estimated when the total catch was only a single individual.

Table XI.

Species	I	II	III	IV	V	VI	Sum chi-square
C. dentatum......	49 + 61 *1.309*	2 + 8 *3.600*	13 + 20 *1.485*	8 + 10 *0.222*	52 + 24 *0.038*	206+173 *2.873*	*9.527*
E. curtus	0 + 0 —	14 + 14 *0.000*	0 + 0 —	6 + 7 *0.077*	12 + 13 *0.040*	394+435 *2.028*	*2.145*
E. bugandensis ...	1 + 3 *1.000*	1 + 3 *1.000*	33 + 26 *0.831*	1 + 1 *0.000*	0 + 2 *2.000*	28 + 31 *0.153*	*4.984*
A. ugandanus	0 + 0 —	1 + 3 *1.000*	4 + 2 *0.667*	5 + 0 *5.000*	11 + 9 *0.200*	28 + 36 *1.000*	*7.867*
A. decoratus	0 + 0 —	2 + 1 *0.333*	2 + 5 *1.286*	0 + 0 —	0 + 0 —	0 + 0 —	*1.619*
C. notabile	0 + 1 —	0 + 0 —	37 + 42 *0.316*	41 + 31 *1.389*	52 + 56 *0.148*	33 + 39 *0.500*	*2.353*
T. maculatus	0 + 0 —	1 + 0 —	0 + 0 —	0 + 2 *2.000*	0 + 0 —	1 + 1 *0.000*	*2.000*
Chi-square sums ..	*2.309*	*5.933*	*4.585*	*8.688*	*2.426*	*6.554*	

Appendix 2.

Some observations on moulting and longevity are presented below. For details on the method employed see page 15. In the tables below, the number of hours that have elapsed since the isolation of the insects are given. For the sub-imagines the total number that moulted after isolation is given. For the imagines, the number alive at the various hours after isolation is shown.

C. corbeti. No experiments carried out.

C. notabile. The times of emergence and moulting are unknown. Longevity experiments carried out on imagines isolated during the dusk peak, indicate that they survive for some time.

Table A. (Insects isolated 1st February 1957. Temperature range measured in the laboratory where the plastic boxes were kept: 20—24°C. Air humidity within the plastic boxes could not be measured.)

No. of hours	0	14	21	39	42	43	61
No. alive	50	50	48	18	12	7	0

Table B. (Insects isolated 23rd July 1958. Temperature range: 22—24°C. Air humidity in the laboratory above 60% rH throughout the experiment.)

No. of hours ..	0	13	22.5	24.5	37	41	42.5	44.5	46.5	47.5	61
No. alive	15	9	9	7	4	4	3	3	2	1	0

Imagines of *C. notabile* are not infrequently found during the day at Jinja.

C. dentatum. The emergence, moulting and longevity not known.

A. ugandanus. Quiescent sub-imagines and imagines have been observed during the first part of the day at Jinja. In the late afternoon only imagines have been found.

Table C. (Sub-imagines from the dusk peak isolated 29th December 1957. Measured air temperature and air humidity range: 23—28°C and 55—80% rH respectively.)

No. of hours ...	0	14.5	15.5	16	16.5	17	25	37	44.5	46.5	48.5	61	65
No. moulted:													
m.	0	0	0	1	2	3							
f.	0	0	9	14	16	16[1]							
No. alive:													
m.	3	3	3	3	3	3	3	3	3	3	3	1	0
f.	17	17	17	17	17	17	16	15[2]	10	10	9	1	0

Table D. (Imagines from the dusk peak — all females — isolated 1st February 1957. Air temperature range measured: 20—24°C.)

No. of hours	0	10.5	14	21.5	39	42	43	61
No. alive	18	18	17	15	3	2	2	0

A male sub-imago isolated at 0800 hrs. on the 17th December 1957 moulted at 1220 hrs., presumably seventeen hours after emergence. A female sub-imago isolated at 0830 on the 30th January 1957 moulted between 1430 hrs. and 1615 hrs. the same day. A female sub-imago isolated at 1930 hrs. on the 21st December 1957, moulted approximately seventeen hours after isolation.

A. decoratus. Imagines only have been seen during the day at Jinja. Sweep net catches taken at sunset yielded imagines only, whereas sweep net catches taken later at night yielded both imagines and sub-imagines. The longevity experiments carried out on this species, met with little success. Evidently the technique employed was unsuitable for this species. Many of the specimens isolated died within twelve hours without showing signs of moulting. None

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[1] One female died as sub-imago.

[2] One female imago escaped.

of the specimens that did show signs of moulting, completed the moulting in captivity. Those that showed signs of moulting showed these signs at or before sunrise.

E. bugandensis and *E. curtus*. Sub-imagines of *E. bugandensis* (but not sub-imagines of *E. curtus*) have been observed shortly after sunrise. Later in the day *E. bugandensis* imagines only have been observed.

Table E. (Sub-imagines of *E. bugandensis* and *E. curtus* isolated in the dusk peak on the 1st February 1957. Temperature range see *Table A* and *D.*)

No. of hours	0	7	7.5	8	8.5	9.5	14	14.5	21.5	39	42.5	61
No. moulted:												
E. bugand. m.	0	0	0	0	0	0	0	4				
—«— f.	0	0	0	0	0	0	0	1				
E. curtus m.	0	0	4	5	9	9[3]						
—«— f.	0	0	0	1	1	2						
No. alive:												
E. bugand. m.	9	9	9	9	9	9	9	7[1]	4	1	0	0
—«— f.	6	6	6	6	6	6	6	6	1[2]	1	1	0
E. curtus m.	11	11	11	11	11	11	11	7	2[4]	0		
—«— f.	3	3	3	3	3	3	3	2	1	0		

The results indicated in *Table E* above, were confirmed by additional experiments and observations. Thus sub-imagines of *E. curtus* were found to have completed ecdysis after eleven hours after sunset. When the ecdysis was not completed then, it normally never occurred, but one individual was observed to complete ecdysis between eleven and fifteen and a half hours after having been isolated. Sub-imagines of *E. curtus* isolated in plastic boxes and left out of doors over night, had normally completed moulting when inspected at sunrise. Similar experiments carried out with *E. bugandensis* sub-imagines showed that few of these had completed their exuviation when inspected at sunrise. They completed their ecdysis shortly after sunrise.

Table F. (Six female imagines of *E. bugandensis* isolated in the dusk peak on the 24th July 1958. Temperature range: 21–24°C. Air humidity range in the laboratory: 68–80% rH.)

No. of hours	0	13	17	18.5	20.5	22.5
No. alive	6	4	3	2	1	0

Table G. (Ten female imagines of *E. bugandensis* isolated in the dusk peak on the 25th August 1958. Temperature and humidity not measured.)

No. of hours	0	13	16.5	18.5
No. alive	10	4	3	0

H. fasciatus. Emergence, moulting and longevity unknown.

P. adusta. For details see Hartland-Rowe (1958).

T. maculatus. Individuals of this species proved difficult to obtain in large numbers for longevity experiments. Some experiments were, however, performed. And the result may serve as an indication.

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[1] Two males died as sub-imagines.

[2] Four females died as sub-imagines.

[3] Two males and one female died without having moulted.

[4] One male killed accidentally.

A female sub-imago was isolated in the dusk peak on the 28th December 1957, and was found on first inspection to have moulted eleven hours afterwards. It was found dead twenty hours after isolation. A male sub-imago and three female sub-imagines were isolated in the evening 24th July 1958. They had all completed moulting when inspected thirteen hours afterwards. The male was found dead after eighteen and a half hours; one female was found dead after twenty-two and a half hours. One was found to have died when inspected after thirty-seven hours, but no inspection was carried out between twenty-three and a half hours and thirty seven hours after isolation. The fourth female was still alive forty-six and a half hours after isolation, but was found dead when inspected sixty one hours after isolation.

Of six sub-imagines isolated in the evening 25th August 1958 four did not complete moulting. The other two (one male and one female) had completed moulting when found dead thirteen hours after the isolation.

T. tinctus. Although piles of dead *T. tinctus* can be found at — and near — the Owen Falls Dam on most mornings, not a single live individual has however been found during the day, although several searches were made for them. It is assumed therefore that *T. tinctus* rarely — if ever — survives the day to fly on a second night. This was confirmed when ten male sub-imagines where isolated at the Dam and brought back to the laboratory in the evening. They had all moulted within four hours of sunset and one was found dead at this time. The remaining nine were all found dead in the morning.

Appendix 3.

Temperature and humidity records from Jinja Airport. The data have kindly been supplied by the East African Meteorological Department at Entebbe.

Mean monthly maximum temperature (°F):

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
1956 ...									81.5	81.9	82.9	82.4
1957 ...	83.2	83.3	82.3	80.7					85.9	85.2	84.1	83.0
1958 ...	85.4	85.1	85.2	84.0								

Average monthly maximum temperature (°F).

85.3	85.4	85.4	82.4	81.0	80.5	80.3	81.2	83.2	84.1	84.8	83.9

Mean monthly relative humidity at 12.00 G.M.T.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
1956 ...									63	60	53	55
1957 ...	52	50	58	68					45	53	53	59
1958 ...	52	50	56	59								

Average monthly relative humidity at 12.00 G.M.T.

50	49	53	63	65	65	59	60	55	55	50	53

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Reference marked [1] not seen.

Figures.

A list of figures is given below. References to the pages on which the figures occur are given in brackets. For explanation, see figures and text.

Fig. 1. An outline map of Jinja and the surrounding district. (page 72).

Fig. 2. The arrangement of the wind vane dial in relation to the direction of the lake shore (page 72).

Fig. 3. The chambers of the metal receptacle in relation to the direction of the lake shore (page 72).

Fig. 4. Various climatic data from the sampling nights in year I (page 72).

Fig. 5. Various climatic data from year II in relation to the age of the moon (page 72). I. (The temperatures and the humidities have been expressed as arithmetic means.)

Figs. 6a & b, Figs. 7a & b. Various climatic data from year II (page 73—74).

Fig. 8. Various climatic data from year II in relation to the age of the moon (page 75). II. Wind (Expressed as the arithmetic means).

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Figs. 20 & 21. The catches of *T. tinctus* and *H. fasciatus* on the various nights in year II (page 78)*.

Fig. 22. The peak frequency histograms of the different species (page 79).

Figs. 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34 & 35. The catches of different species of mayflies in year II (page 80—85)*.

Figs. 36, 37, 38a & b, 39, 40, 41a & b, 42, 43, 44, 45a & b, 46a & b. The catches* of the different species of mayflies during year II in relation to the age of the moon (page 86—87).

Fig. 47. The times of the first captures of *E. curtus* imagines (catches made during the first two hours of the night excepted) in relation to the temperature as recorded at midnight (page 87).

Fig. 48. The catches* of mayflies (year II) in relation to climatic factors. The catches are those of the first hour of the night where not indicated by (11) the name of the species and the stage of the species. The species and stages have been indicated by their initials (page 87).

Fig. 49. The catches* of mayflies (year II) in relation to climatic factors. In the sunset temperature diagram, the nightly catches* of mayflies have been employed. In the sunrise temperature diagram, the catches* of the last eleven hours of the night have been used. In the relative humidity at midday diagram, the nightly catches* have been used. And in the wind diagram, the catches* of mayflies during the first hour of the night have been employed. Otherwise as Fig. 48. (Page 88).

Fig. 50. Various flight activity patterns exhibited by some of the species of mayflies studied. The sub-imaginal period has been indicated by dashed or dotted lines. The imaginal period has been indicated by solid lines (page 88).

* The catches equal approximately half the total catches made by the light trap (cf. page 13).

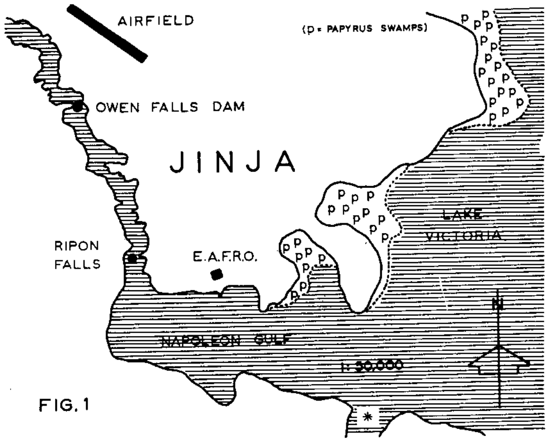


FIG. 1

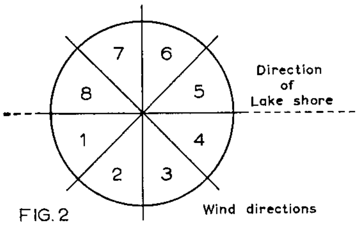


FIG. 2

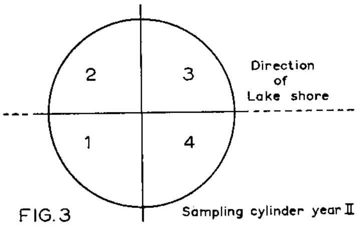


FIG. 3

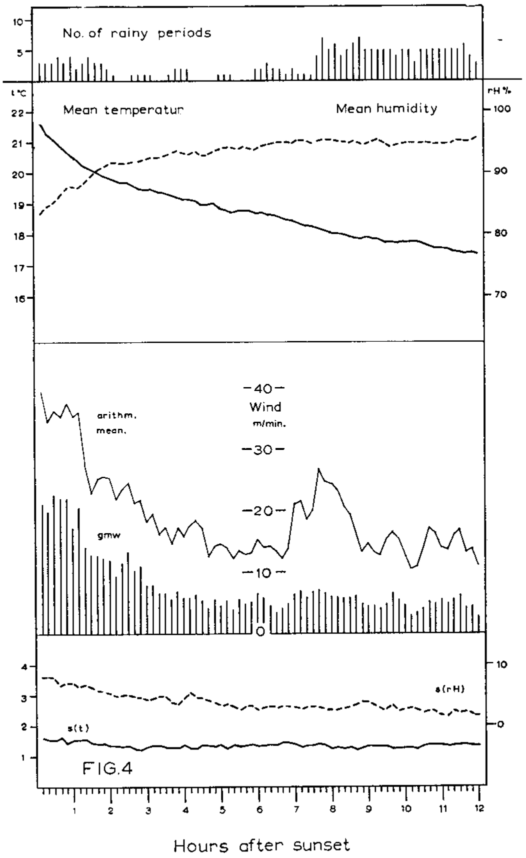


FIG. 4

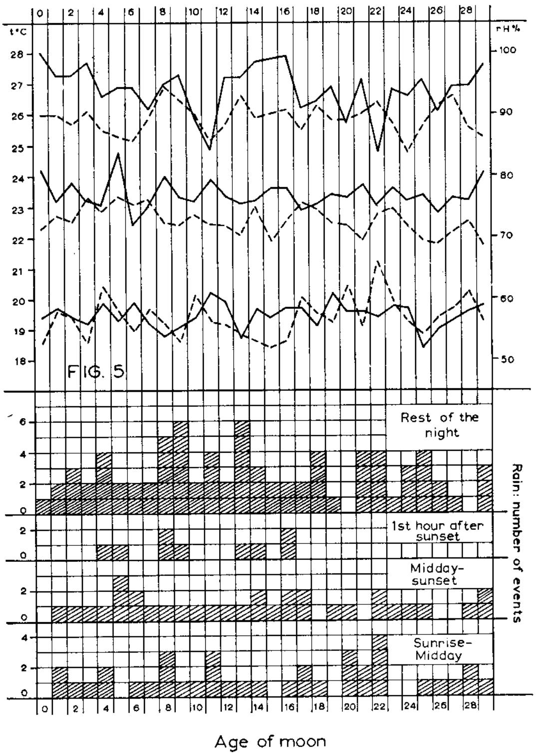


FIG. 5

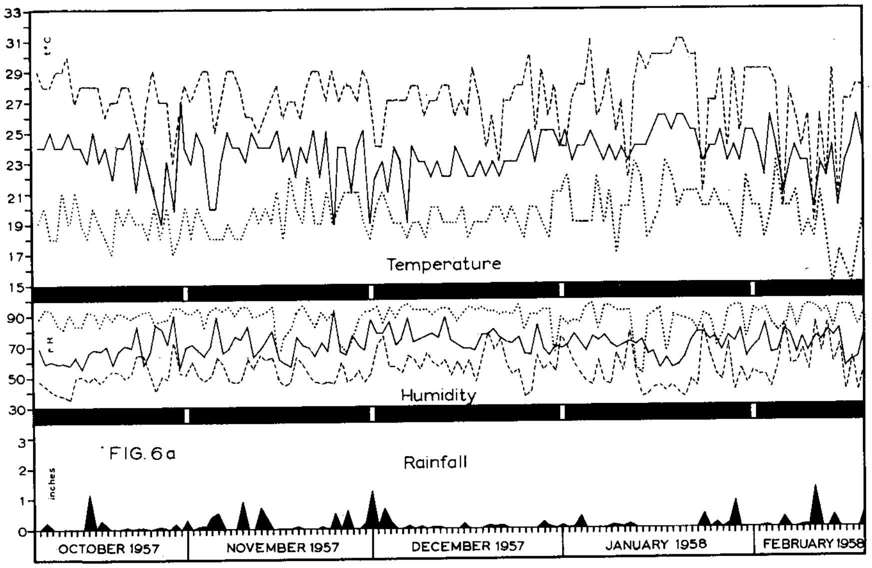


FIG. 6a
33
31
29
27
25
23
21
19
17
15
t°C
Temperature
90
70
50
30
r H
Humidity
3
2
1
0
inches
Rainfall
OCTOBER 1957
NOVEMBER 1957
DECEMBER 1957
JANUARY 1958
FEBRUARY 1958

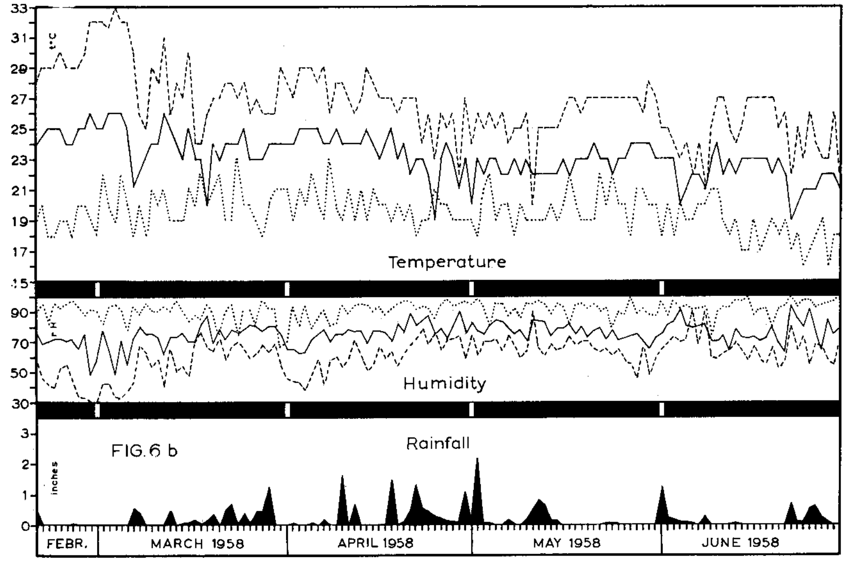


FIG. 6 b
33
31
29
27
25
23
21
19
17
15
t°C
Temperature
90
70
50
30
r H
Humidity
3
2
1
0
inches
Rainfall
FEBR.
MARCH 1958
APRIL 1958
MAY 1958
JUNE 1958

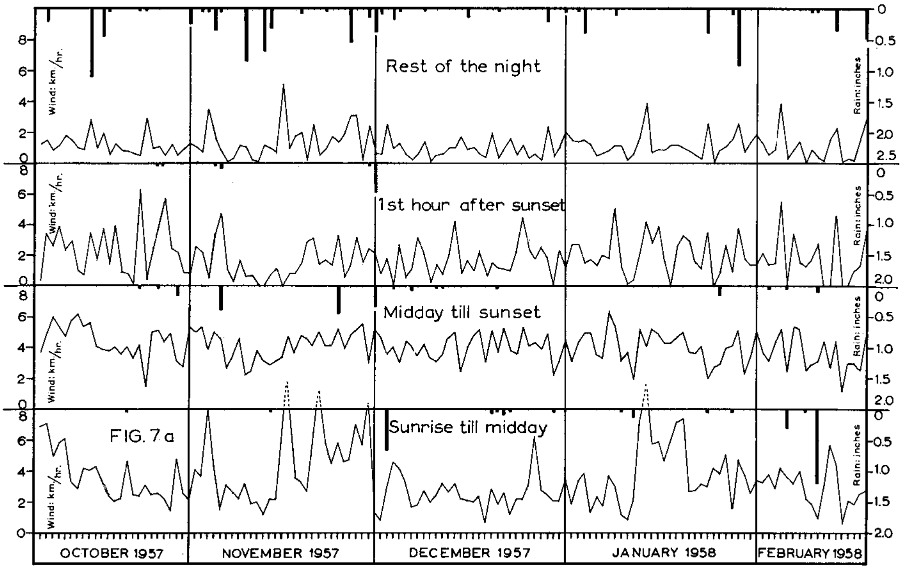


FIG. 7a

Rest of the night
1st hour after sunset
Midday till sunset
Sunrise till midday
Wind: km/hr.
Rain: inches
0
2
4
6
8
0
0.5
1.0
1.5
2.0
2.5
OCTOBER 1957
NOVEMBER 1957
DECEMBER 1957
JANUARY 1958
FEBRUARY 1958

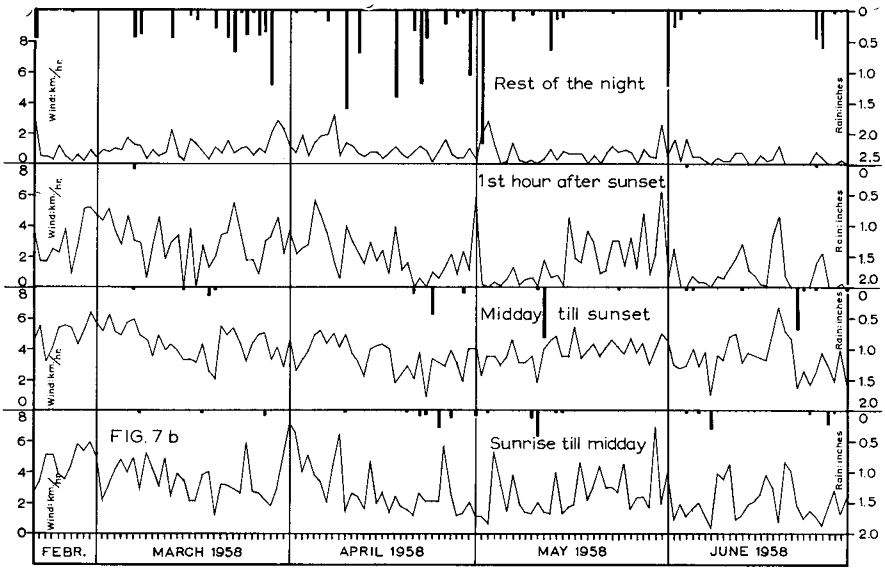


FIG. 7 b

Rest of the night
1st hour after sunset
Midday till sunset
Sunrise till midday
Wind: km/hr.
Rain: inches
0
2
4
6
8
0
0.5
1.0
1.5
2.0
2.5
FEBR.
MARCH 1958
APRIL 1958
MAY 1958
JUNE 1958

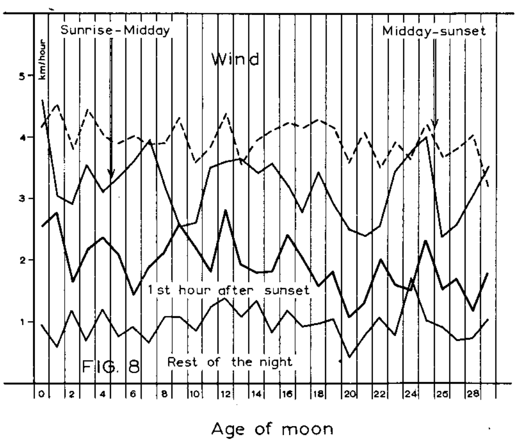


FIG. 8

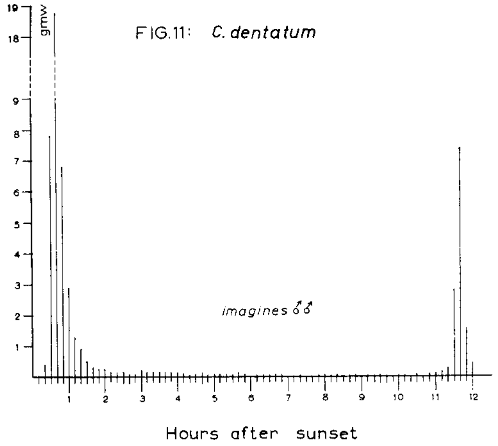


FIG.11: *C. dentatum*

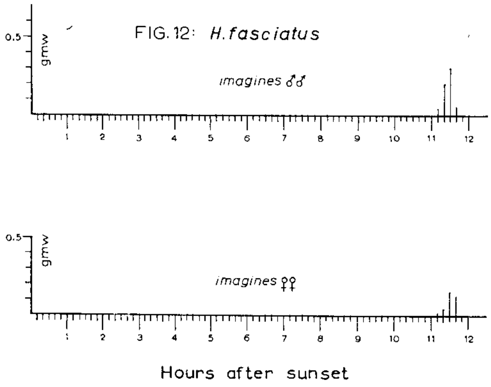


FIG. 12: *H. fasciatus*

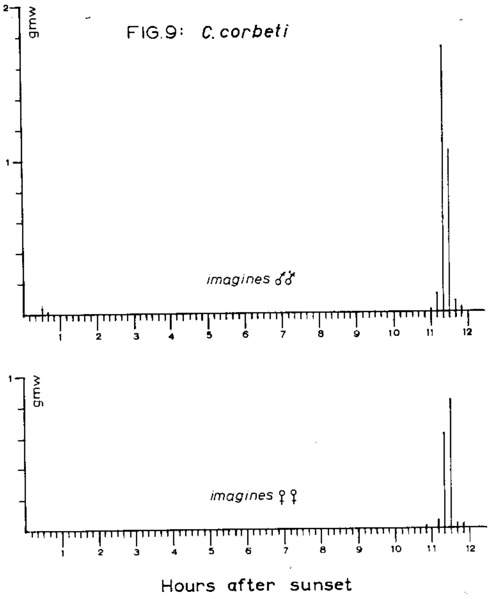


FIG.9: *C. corbeti*

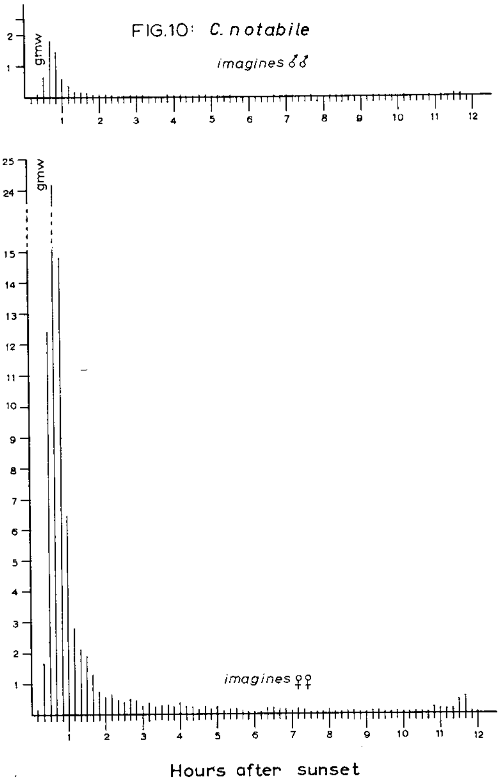


FIG.10: *C. notabile*

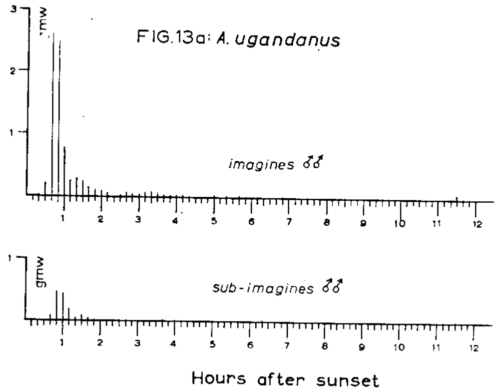


FIG.13a: *A. ugandanus*

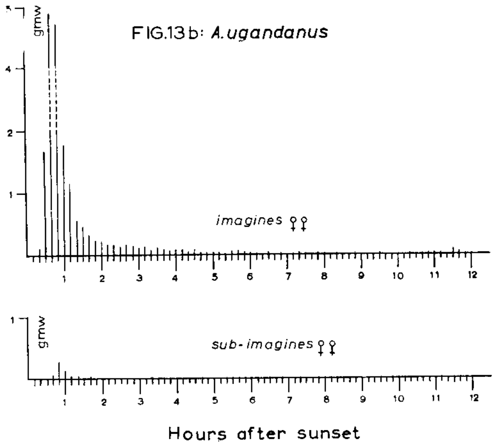


FIG.13b: *A. ugandanus*

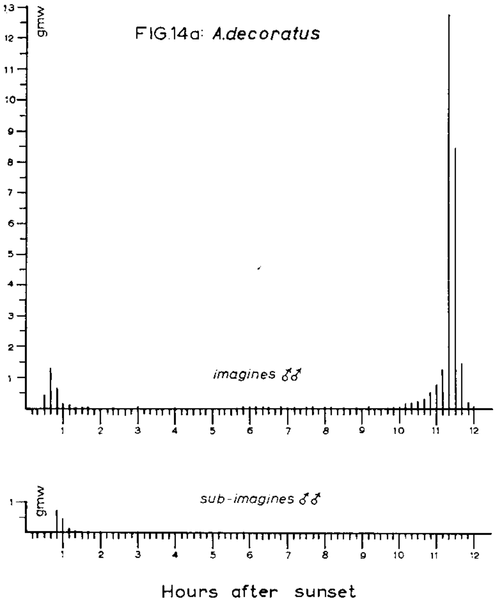


FIG.14a: *A. decoratus*

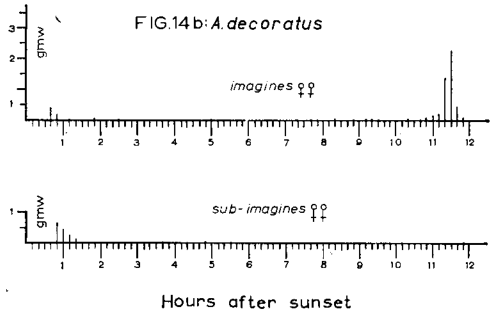


FIG.14b: *A. decoratus*

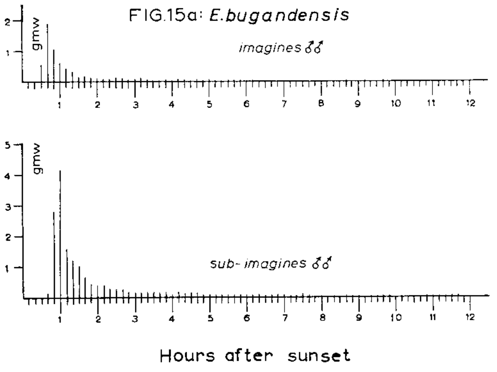


FIG.15a: *E. bugandensis*

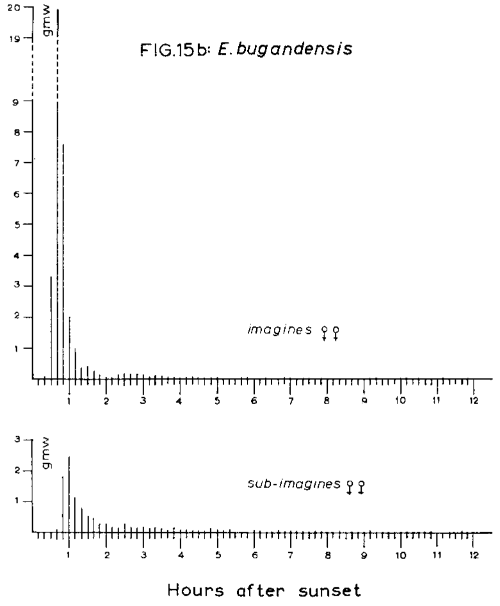


FIG.15b: *E. bugandensis*

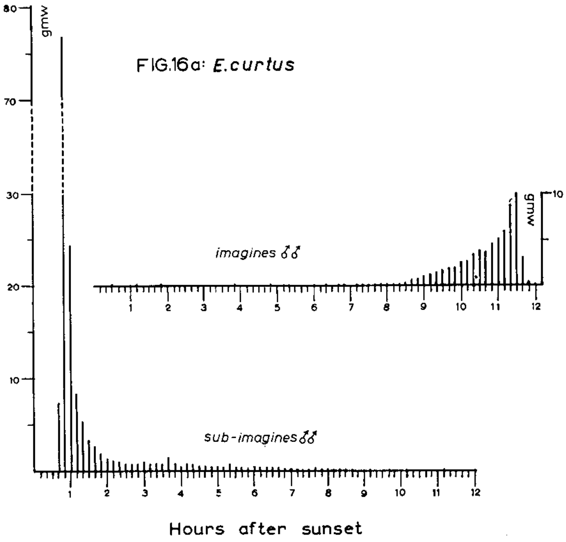


FIG.16a: *E.curtus*

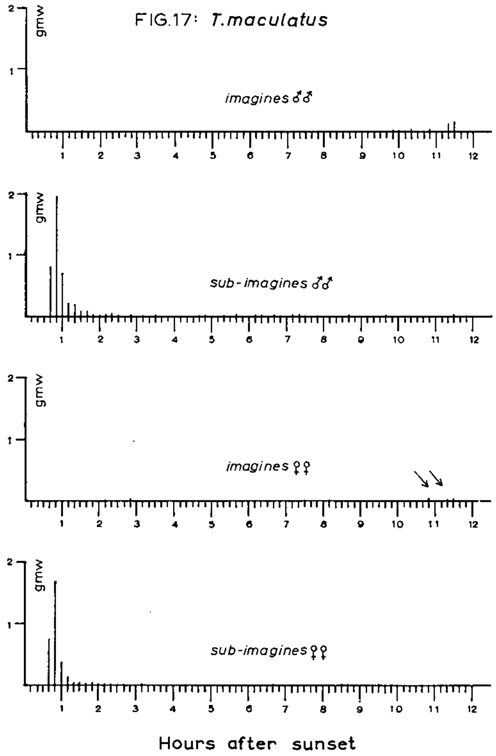


FIG.17: *T.maculatus*

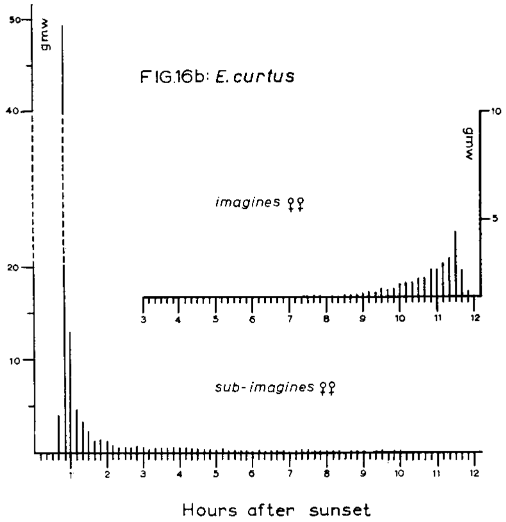


FIG.16b: *E. curtus*

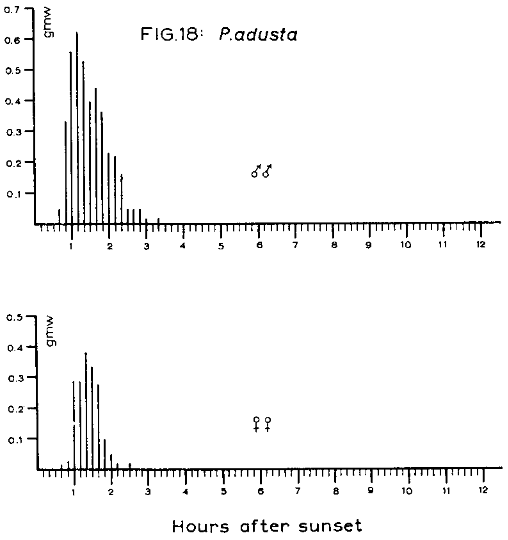
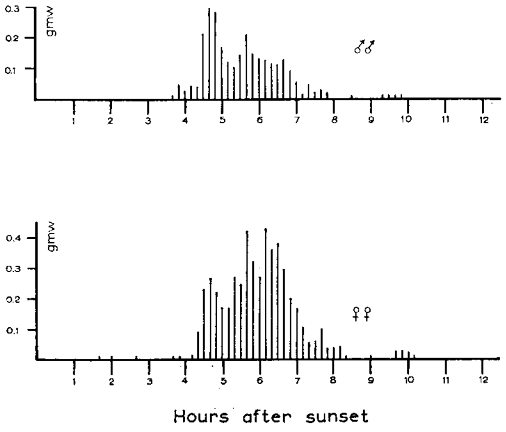


FIG.18: *P.adusta*

FIG.19: *T. tinctus*



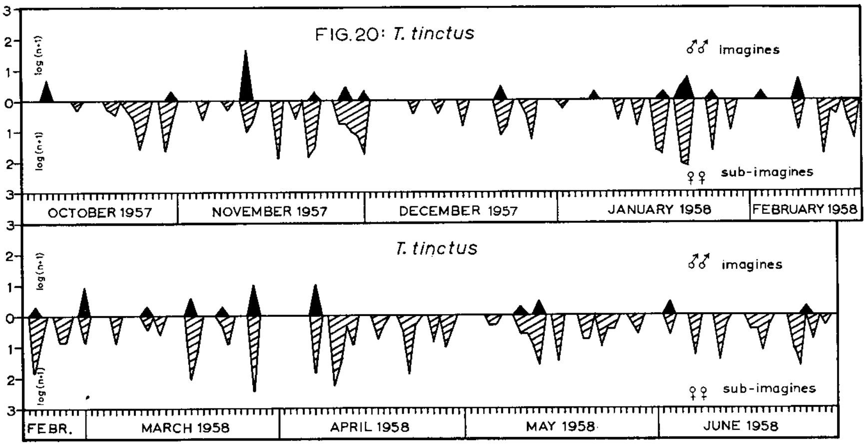


FIG. 20: *T. tinctus*

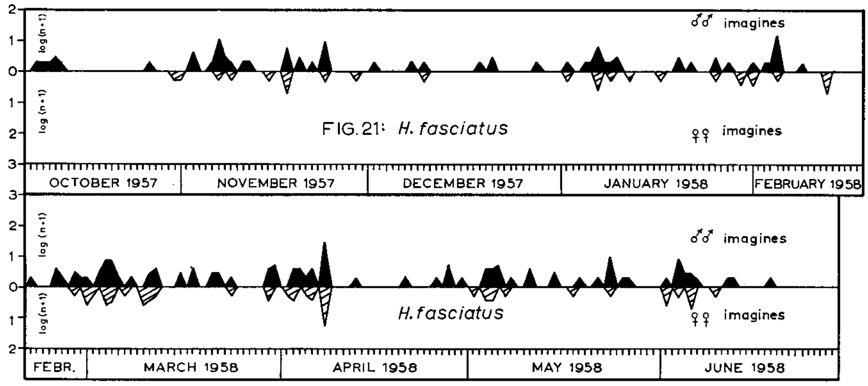
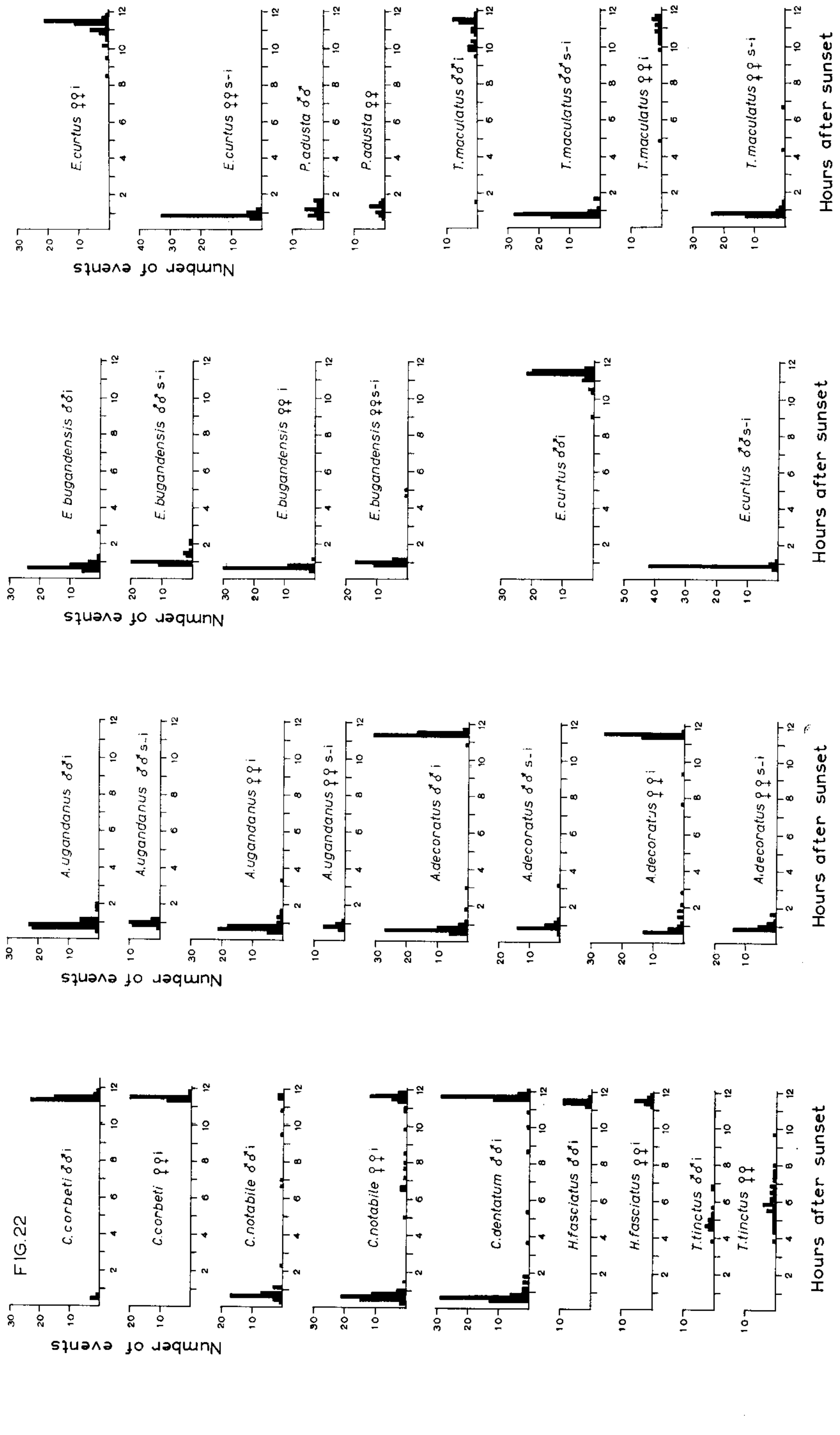


FIG. 21: *H. fasciatus*

FIG. 22


C.corbeti ♂♂ i
C.corbeti ♀♀ i
C.notabile ♂♂ i
C.notabile ♀♀ i
C.dentatum ♂♂ i
H.fasciatus ♂♂ i
H.fasciatus ♀♀ i
T.tinctus ♂♂ i
T.tinctus ♀♀
A.ugandanus ♂♂ i
A.ugandanus ♂♂ s-i
A.ugandanus ♀♀ i
A.ugandanus ♀♀ s-i
A.decoratus ♂♂ i
A.decoratus ♂♂ s-i
A.decoratus ♀♀ i
A.decoratus ♀♀ s-i
E.bugandensis ♂♂ i
E.bugandensis ♂♂ s-i
E.bugandensis ♀♀ i
E.bugandensis ♀♀ s-i
E.curtus ♂♂ i
E.curtus ♂♂ s-i
E.curtus ♀♀ i
E.curtus ♀♀ s-i
P.adusta ♂♂
P.adusta ♀♀
T.maculatus ♂♂ i
T.maculatus ♂♂ s-i
T.maculatus ♀♀ i
T.maculatus ♀♀ s-i
Number of events
Hours after sunset
2
4
6
8
10
12
10
20
30
40
50

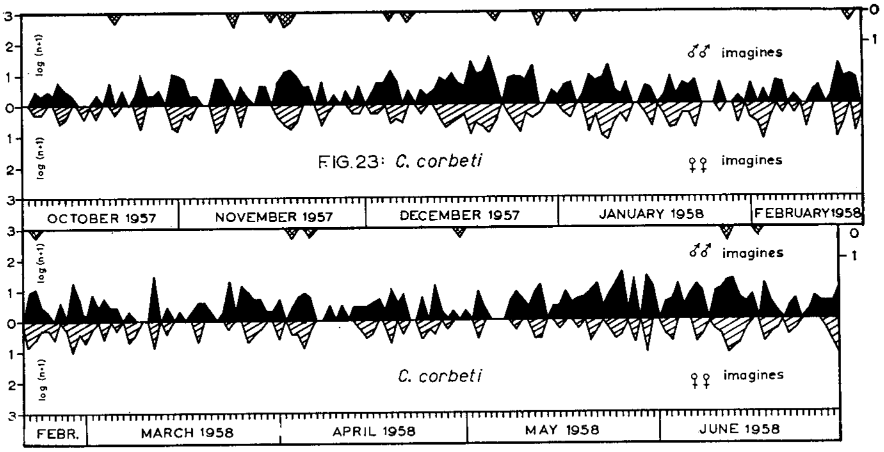


FIG.23: *C. corbeti*

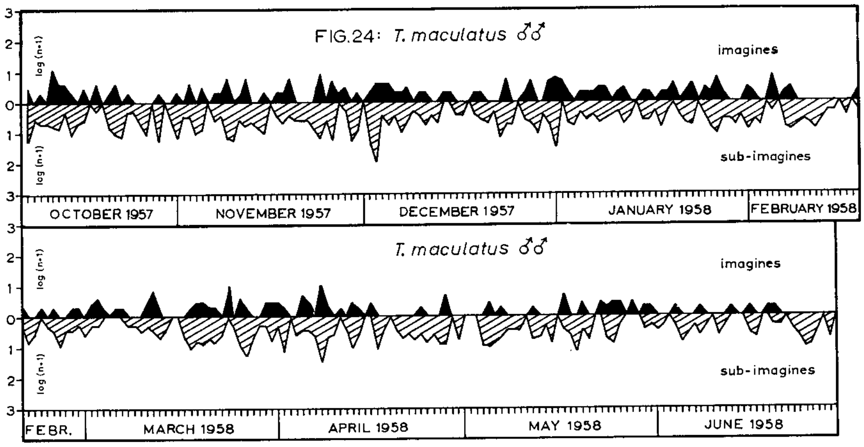


FIG.24: *T. maculatus* ♂♂

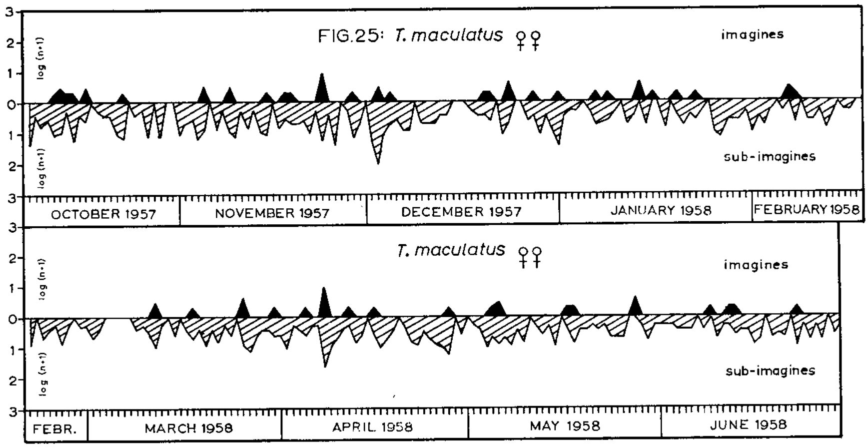


FIG.25: *T. maculatus* ♀♀

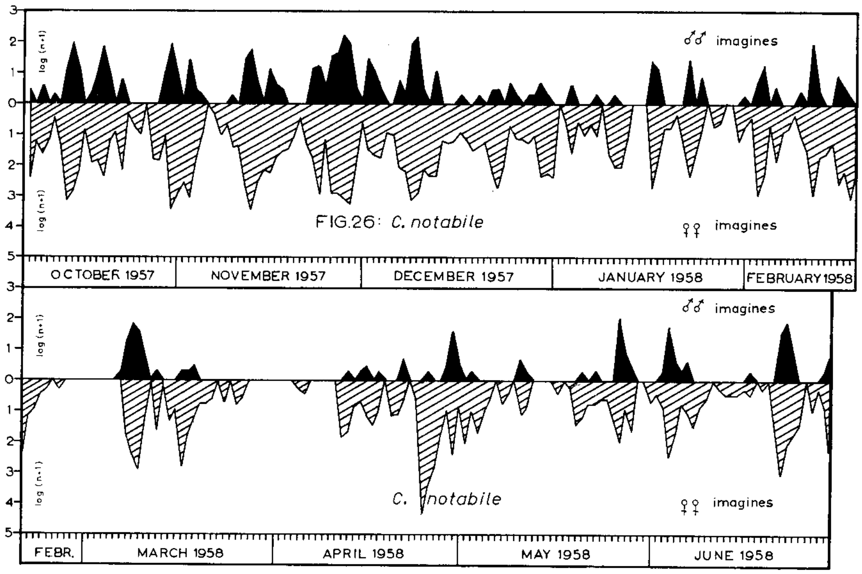


FIG.26: *C. notabile*

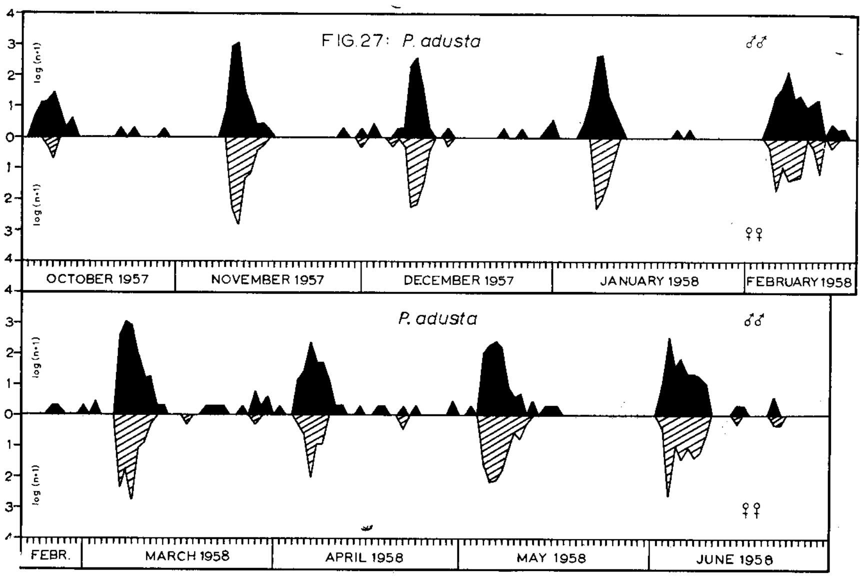


FIG.27: *P. adusta*

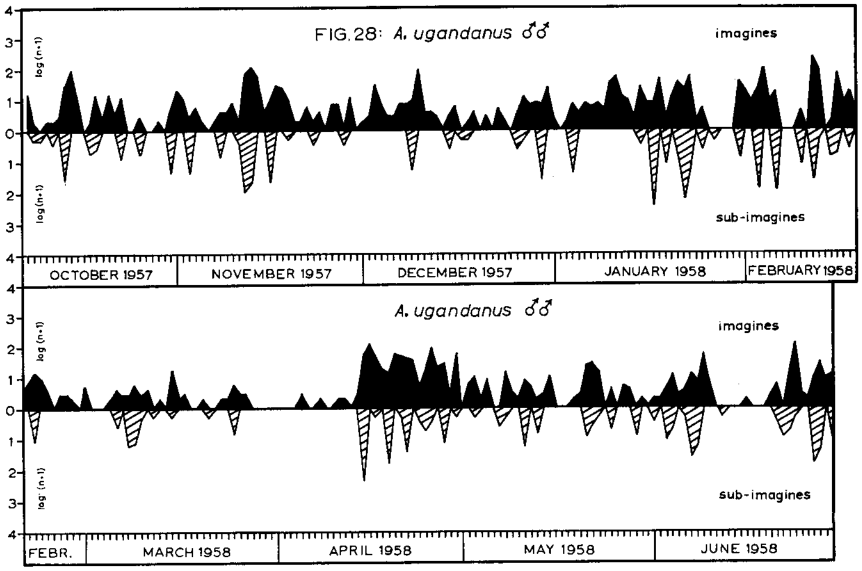


FIG. 28: *A. ugandanus* ♂♂

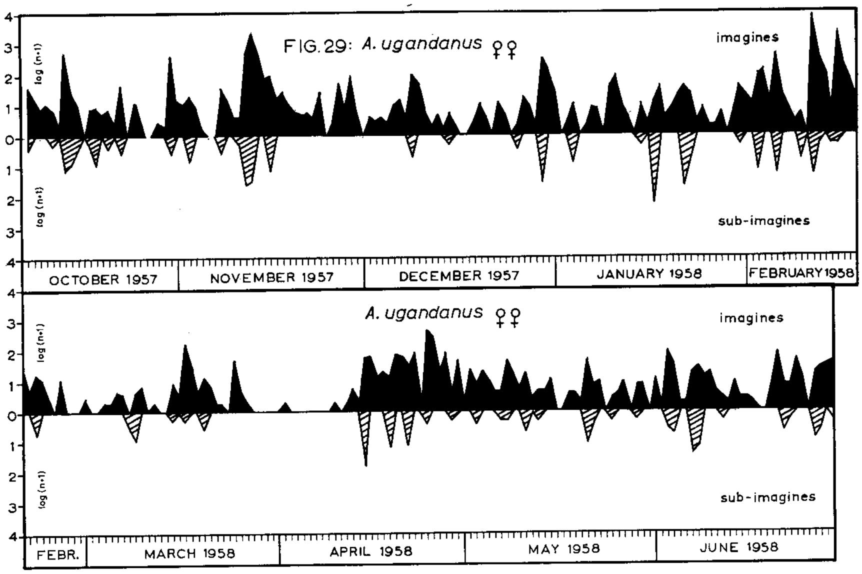


FIG. 29: *A. ugandanus* ♀♀

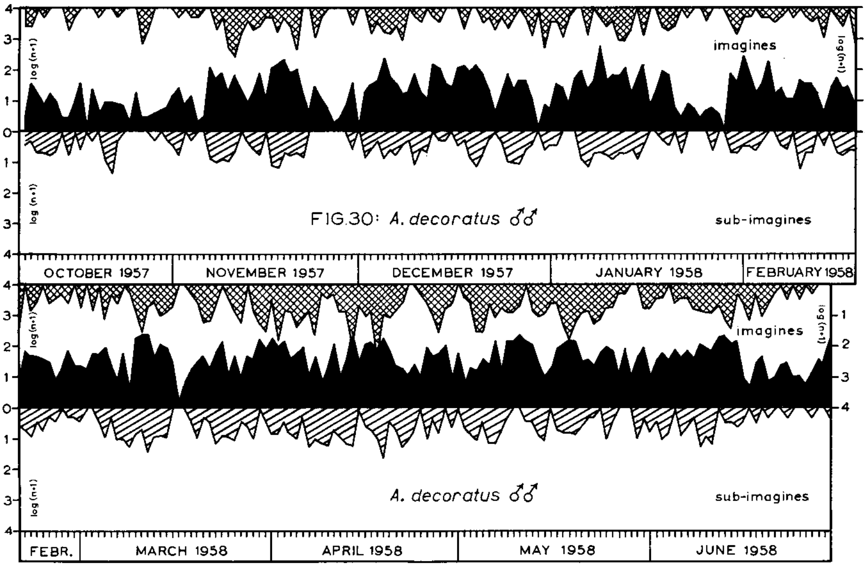


FIG. 30: *A. decoratus* ♂♂

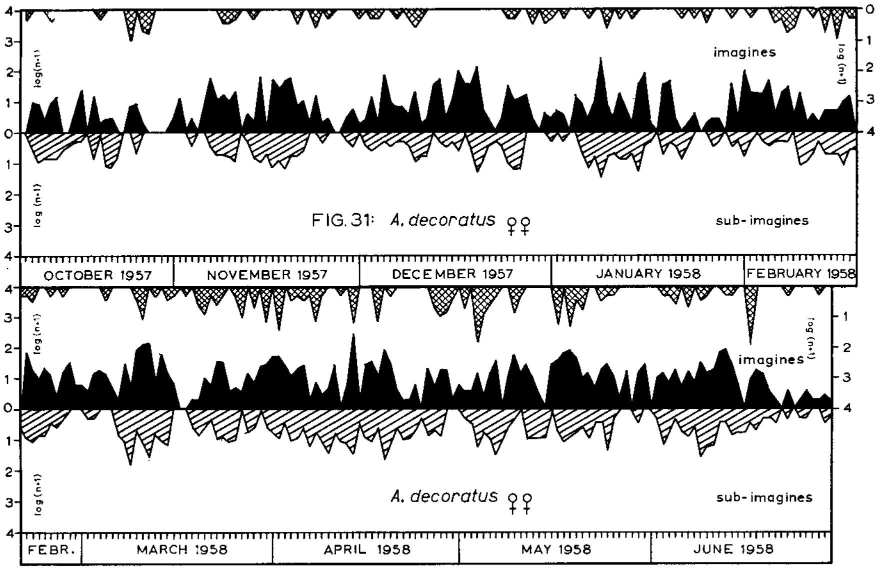


FIG. 31: *A. decoratus* ♀♀

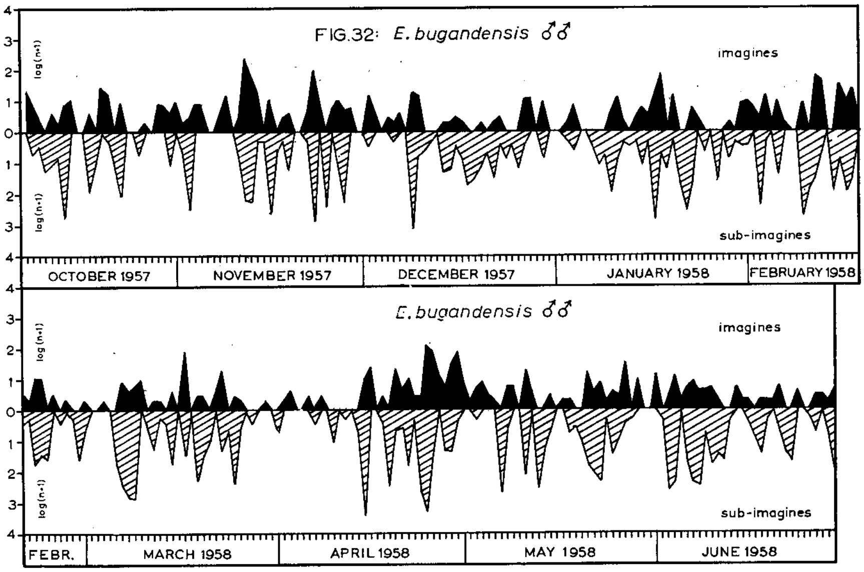


FIG.32: *E. bugandensis* ♂♂

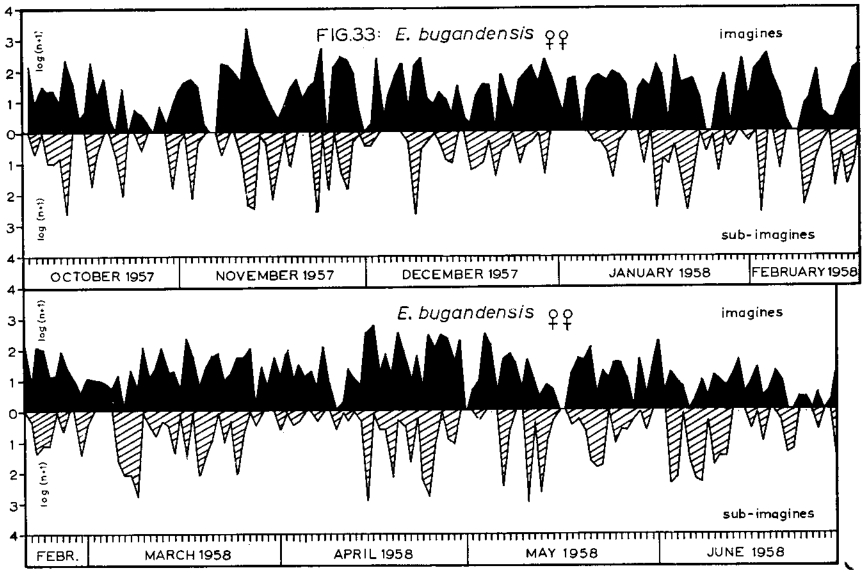


FIG.33: *E. bugandensis* ♀♀

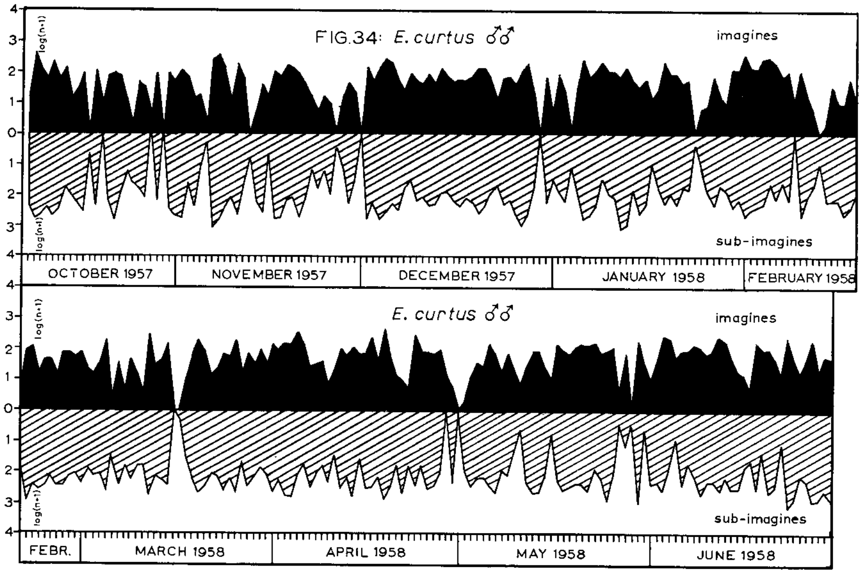


FIG. 34: *E. curtus* ♂♂

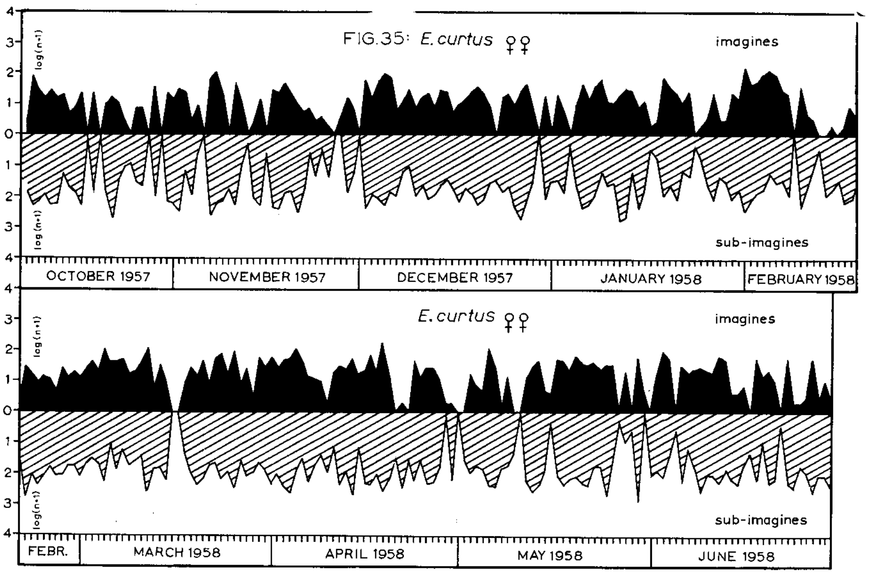
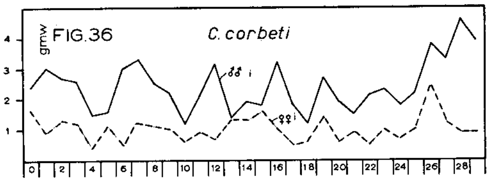
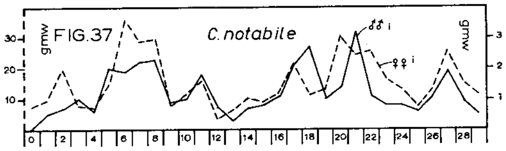
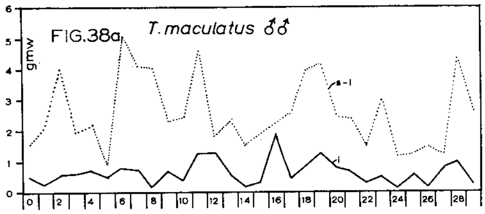
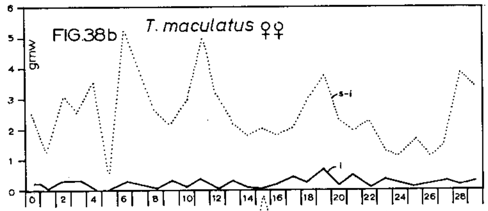


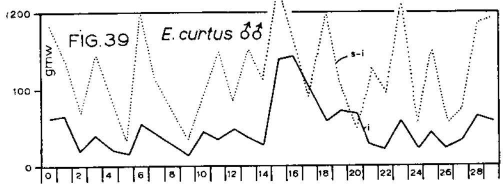
FIG. 35: *E. curtus* ♀♀

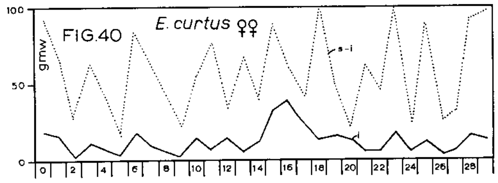




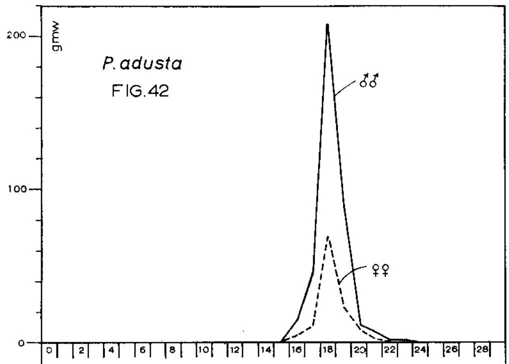


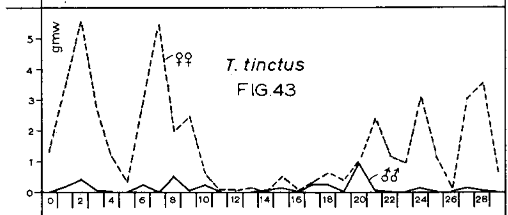


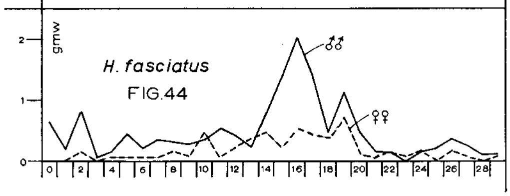




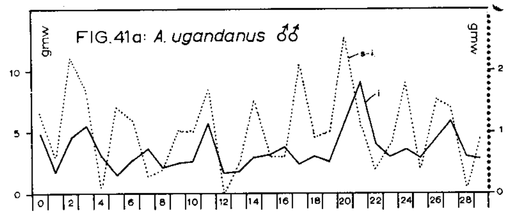
Age of moon

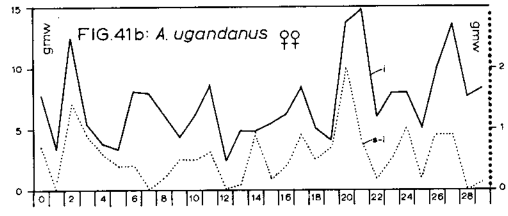






Age of moon





Age of moon

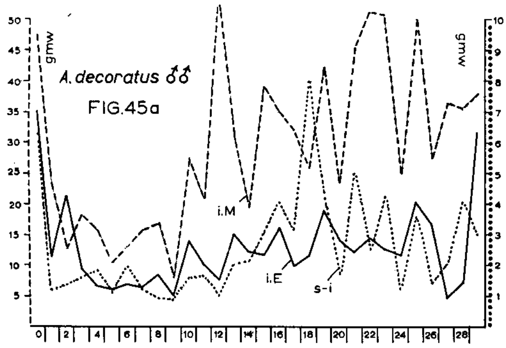


FIG.45a

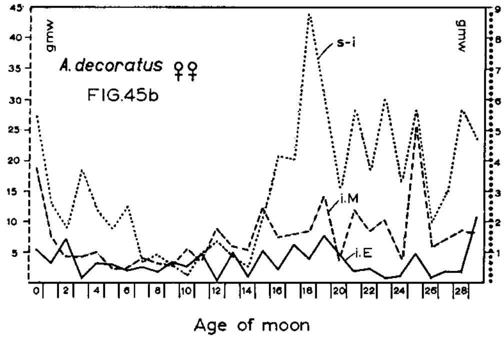


FIG.45b

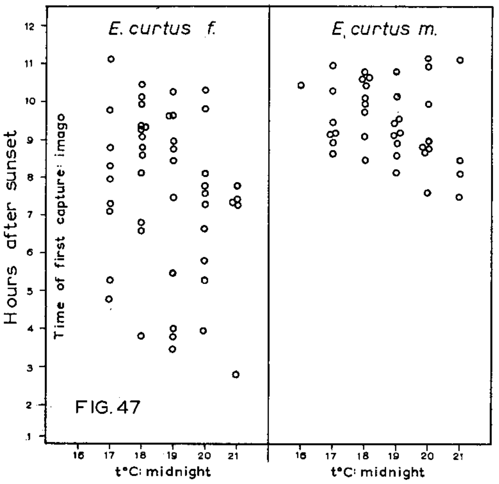


FIG. 47

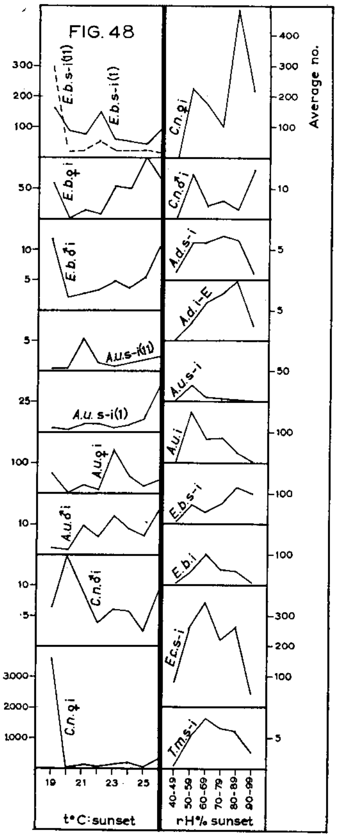


FIG. 48

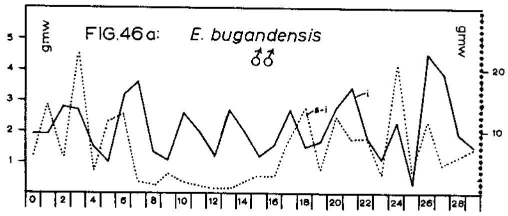


FIG.46a: E. bugandensis ♂♂

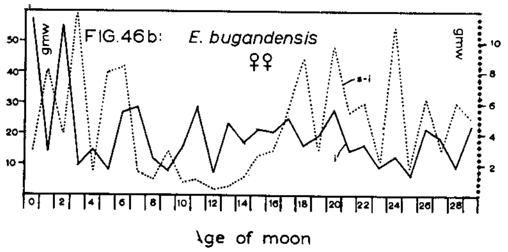
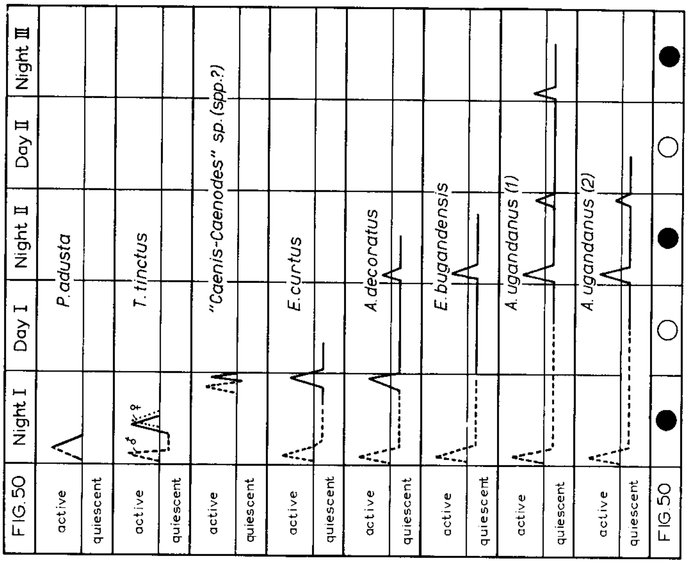
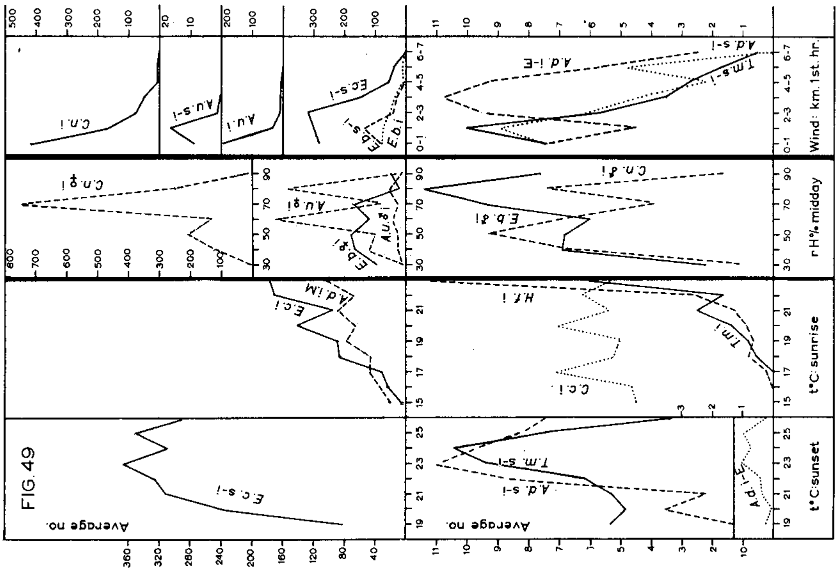


FIG.46b: E. bugandensis ♀♀





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