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OBSERVATIONS
ON CHOROTERPES CURTUS
(KIMMINS) (EPHEMEROPTERA)
AT JINJA, UGANDA

BY

AUDFINN TJØNNELAND

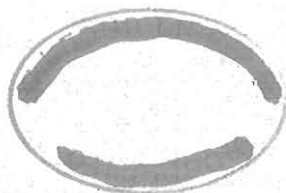
Zoological Laboratory

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ABSTRACT

The African mayfly *Choroterpes curtus* (KIMMINS) is known to show a bimodal flight activity at Jinja, Uganda, where extensive light trap catches of this species were made in 1957–58. The dusk peak is made up of subimagines and occurs at a lower light intensity than does the dawn peak, which is made up of imagines. The dusk peak also shows a lower catch sex ratio — ($\sigma\sigma/\rho\rho$) — than does the dawn peak. The dusk peak of females slightly precedes the dusk peak of males. At dawn the activity peak of males slightly precedes that of the females. The observed asymmetry in the spacing of the peaks in relation to solar midnight can be explained if CORBET's model (1965) is adopted, taking into consideration also the changes in the efficiency of a light trap at dusk and dawn.

The few imagines caught during the first hours after sunset are regarded as consisting of survivors from an older emergence group and insects that have emerged and moulted early the same evening.

It has been suggested that the ratio \bar{x}/M_w may be useful as a rough and easily calculated indication of the consistency of a series of nightly samples. If this ratio is used, it is imperative that either \bar{x} or M_w is also given to enable the readers to form an opinion of the nightly mean catches of the species.

INTRODUCTION

Using a Robinson mercury vapour light trap, TJØNNELAND (1960) recorded the flight activity of certain nocturnal *Ephemeroptera* at Jinja, Uganda. During the first year (1956–57) the trap was run every seventh night. Each of the resulting 52 sampling nights was divided into 10-minute sampling periods, each night yielding 72 such sampling periods. During the second year (1957–58) the trap was run every night for nine synodic months and it was emptied twice per night: the first time one hour after sunset and the second time at sunrise. The procedure has been described in a previous paper (TJØNNELAND, 1960), which also lists the environmental factors recorded.

The present paper provides a further analysis of the catches of the mayfly *Choroterpes curtus* (KIMMINS). Both subimagines and imagines of this species are readily caught by a light trap and the species shows a continuous emergence as this term has been defined by CORBET (1964).

Subimagines of the species have been observed to emerge at dusk from the Napoleon Gulf (TJØNNELAND, 1960). The subimagines fly after sunset and light trap catches of subimagines generally reach a maximum 40 to 50 minutes after sunset. Having reached the maximum, the decline of the subsequent 10-minutes'

catches of subimagines is at first rapid, but subimagines may be caught for a substantial part of the night. Moulting takes place during the night and imagines fly during the last part of the night, the maximum catches occurring before sunrise. Some imagines are caught between sunset and midnight, and they have been further discussed in the present paper. The effect of some environmental factors on the catches is also dealt with. The effect these factors may have in obscuring an interpretation of the emergence pattern from catch data has been briefly considered.

CATCH DATA

CORBET (1964) lists and discusses the following types of emergence: continuous, rhythmic, sporadic and seasonal emergence. A series of nightly catches extending over nine synodic months has shown that *C. curtus* must be classified as having a continuous type of emergence (TJØNNELAND, 1960; CORBET, 1964). This is also brought out quite well in Table 1 which gives the average nightly catch, expressed both as the arithmetic mean (\bar{x}) and as WILLIAMS' (1935) mean (M_w) for each of the synodic months.

Table 1. The mean nightly catches (expressed as \bar{x} and M_w) of *C. curtus* for each of a series of nine synodic months during 1957–1958.

		7.x- 4.xi 1957	5.xi- 4.xii 1957	5.xii- 2.i 1957/8	3.i- 1.ii 1958	2.ii- 3.iii 1958	4.iii- 1.iv 1958	2.iv- 1.v 1958	2.v- 31.v 1958	1.vi- 29.vi 1958
♂♂ i	\bar{x}	151.6	163.6	149.9	181.7	152.2	203.8	183.1	139.5	185.5
	M_w	65.5	56.5	103.5	91.4	75.0	121.0	82.0	82.1	110.0
	$\frac{\bar{x}}{M_w}$	2.31	2.90	1.45	1.99	2.03	1.68	2.23	1.70	1.69
♀♀ i	\bar{x}	31.2	43.7	34.3	47.5	47.9	69.1	56.7	48.9	44.6
	M_w	14.6	14.1	21.0	21.8	18.6	42.4	21.5	21.3	17.0
	$\frac{\bar{x}}{M_w}$	2.14	3.10	1.63	2.18	2.58	1.63	2.64	2.30	2.62
♂♂ s-i	\bar{x}	414.1	471.7	367.0	417.6	380.8	380.4	449.8	442.9	629.7
	M_w	150.0	153.5	228.6	200.8	216.8	214.9	229.3	190.5	314.0
	$\frac{\bar{x}}{M_w}$	2.76	3.07	1.61	2.08	1.76	1.77	1.96	2.32	2.01
♀♀ s-i	\bar{x}	186.7	191.1	170.8	197.6	178.5	191.8	270.9	275.2	256.6
	M_w	65.5	55.7	105.0	81.6	103.1	105.3	134.4	101.7	133.5
	$\frac{\bar{x}}{M_w}$	2.85	3.43	1.63	2.42	1.73	1.82	2.02	2.71	1.92

In Table 1 the ratio \bar{x}/M_w has also been given. These ratios are easily calculated and when supplied with the corresponding M_w value, would seem to give a better idea of the consistency of the catches than when the M_w value is given alone. The \bar{x}/M_w ratio does give an idea of the variation of the catches. It is obvious that if the nightly catches of a given stage and sex of *C. curtus* do not vary within the synodic month, \bar{x} will equal M_w and the ratio \bar{x}/M_w will equal 1. A variation in the size of the nightly catches will increase the ratio and a pronounced variation will result in rather high ratios, as will be seen from the following set of examples:

Total monthly catch = 900 individuals. Number of nights = 30. \bar{x} = 30 individuals per night.

Number of nights	catch per night \bar{x}	M_w	\bar{x}/M_w
30	30	30	1.0
27 3	33 3	24.3	1.2
25 5	36 none	18.8	1.6
20 10	45 none	11.8	2.5
15 15	60 none	6.8	4.4
10 20	90 none	3.5	8.6
5 25	180 none	1.38	21.7
1 29	900 none	0.254	118.1

If the catches made during the nine synodic months are compared, it is seen that the M_w values are relatively high, showing abundance. Furthermore, the \bar{x}/M_w ratios are rather low, showing little variation of the catches.

The \bar{x}/M_w ratios, it is noticed, reached a maximum in all four recorded catch groups in the period extending from 5th November to 4th December 1957. Similarly, the ratios reached a minimum for all four catch groups during the period extending from 5th December 1957 to 2nd January 1958, but as far as the ♀♀ imagines are concerned another minimum is reached from 4th March to 1st April 1958.

The mean values and the ratio have also been calculated for the catches made during the weekly sampling during the first year. It should be noted that females (subimagines as well as imagines) were not identified in the catches made during the first seven sampling nights. Males of *C. curtus* were identified for all 52 nights. Hence two sets of values have been given for the males. One set comprises the 52 sampling nights, the other set comprises the last 45 sampling nights only. The latter set of values is comparable with the set of values given for the females.

Table 2. The mean nightly catches (expressed as \bar{x} and M_w) of *C. curtus* for weekly sampling nights during 1956–1957. The 52 sampling nights cover a period from 14th September 1956 to 7th September 1957. The 45 sampling nights cover a period from 2nd November 1956 to 7th September 1957.

	\bar{x}	M_w	$\frac{\bar{x}}{M_w}$
♂♂ i (n = 52)	195.4	55.3	3.53
♂♂ i (n = 45)	204.2	64.3	3.18
♀♀ i (n = 45)	68.2	16.3	4.18
♂♂ s-i (n = 52)	623.9	159.8	3.90
♂♂ s-i (n = 45)	692.6	217.2	3.19
♀♀ s-i (n = 45)	308.2	93.3	3.30

If Table 1 and Table 2 are compared, it is seen that the fluctuation of the size of the catches was generally more pronounced during the first year of sampling (Year I), when the catches were obtained once a week, than during the second year of sampling (Year II), when samples were taken every single night for 266 nights. The mean catches (\bar{x}) per night were higher in Year I, and this applies to both sexes and stages (TJØNNELAND, 1960).

In trying to determine the emergence pattern of larvo-aquatic insects by indirect means — such as a light trap — there are certain relevant requirements. It is important that the newly emerged insect can be readily recognized or, failing this, the total adult life span of the insect must be a short one (CORBET & TJØNNELAND, 1955; CORBET, 1964). The mayfly *C. curtus* fulfils both requirements. Also, the observation must needless to say be continuous; the catch records from Year I, when the trap was run every seventh night, yield no reliable information as far as the type of emergence is concerned.

As previously stated, most imagines of *C. curtus* are caught shortly before sunrise. These are recruited from sub-imagines which emerged the previous evening. A few imagines have, however, been caught shortly after sunset. During the 52 sampling nights of Year I, only one imago (a male) was caught during the first hour after sunset, while in all 22 imagines (all males) were caught between sunset

Table 3. *The average nightly catch of imagines taken during the first hour after sunset.*

Sex	Year I		Year II	
	<i>n</i>	\bar{x}	<i>n</i>	\bar{x}
♂♂	52	0.019	266	0.541
♀♀	45	0	266	0.113

and midnight. Some of these may well represent the same emergence group as the subimagines flying in the evening peak — *i.e.* individuals that have undergone ecdysis earlier than usual.

During Year II a method of subsampling was employed to cope with the samples — for details cf. TJØNNELAND, 1960 — and the figures obtained for the first catching hour of the night are therefore not quite so reliable, but 144 male imagines and 30 female imagines were recorded from this period. It is not possible to say how many imagines entered the trap before midnight in Year II as the imagines caught after the first catching hour were pooled.

It is interesting that the mean catches (\bar{x}) of imagines taken during the first hour after sunset are higher for Year II than for Year I. This has been shown in Table 3.

The highest number of imagines caught during the first hour of sampling in any one night was 86 males and 20 females. Both maxima occurred on the same night: 4th March 1958. This was a night with an unusually high evening temperature (26° C) following a very hot day (33° C) with a low air humidity. The catches taken on March 4th 1958 contribute markedly to the averages in Table 3, but even if the catches from this somewhat unusual night are excluded, the mean catches of imagines taken during the first hour after sunset are still higher for Year II than for Year I.

Table 4. *The number of nights when an imago or imagines of C. curtus were present in the subsample from the first hour after sunset in Year II. The average nightly catch (\bar{x}) per night group applies to the insects found in the subsample only.*

	Number of nights	\bar{x}	
		♂♂	♀♀
Only a single imago found in subsample:			
Male	13	1	0
Female	2	0	1
More than one imago found in subsample:			
Males only	3	3	0
Females only	0		
Both males and females	3	16.7	4.33

(Since these figures applies to the imagines found in the subsample, they are only approximately half the total catches of imagines.)

Table 5. The catch sex ratios of *C. curtus* for Year I and Year II. For further explanation see text.

Stage	Year I (n = 45)	Year II (n = 266)	Year II. Imagines caught during the first hour after sunset
Subimagines	2.25	2.05	
Imagines	2.99	3.56	4.80

Evening catches of imagines of *C. curtus* are not limited to nights following hot days. Catches have also been made after cool and humid days. If the imagines of *C. curtus* flying shortly after sunset are considered as a group, it is likely that the group is heterogeneous as will be discussed later.

Table 4 shows the number of nights in Year II when one or more imagines, were present in the subsample from the first hour after sunset.

As subsampling was employed, it is obvious that the number of nights when imagines were caught by the trap must be higher than indicated by Table 4.

In Table 5 the catch sex ratios — here expressed as $\sigma\sigma/\varphi\varphi$ — have been given for subimagines and imagines for both years. The imagines caught during the first hour after sunset have been regarded as a separate entity.

In both years imagines show a higher catch sex ratio than subimagines. Thus as the emerged population increases in age, fewer females are caught in proportion to the capture of males. The catch sex ratio of the imagines caught before midnight is particularly high. (In Year I, as previously stated, all the imagines caught

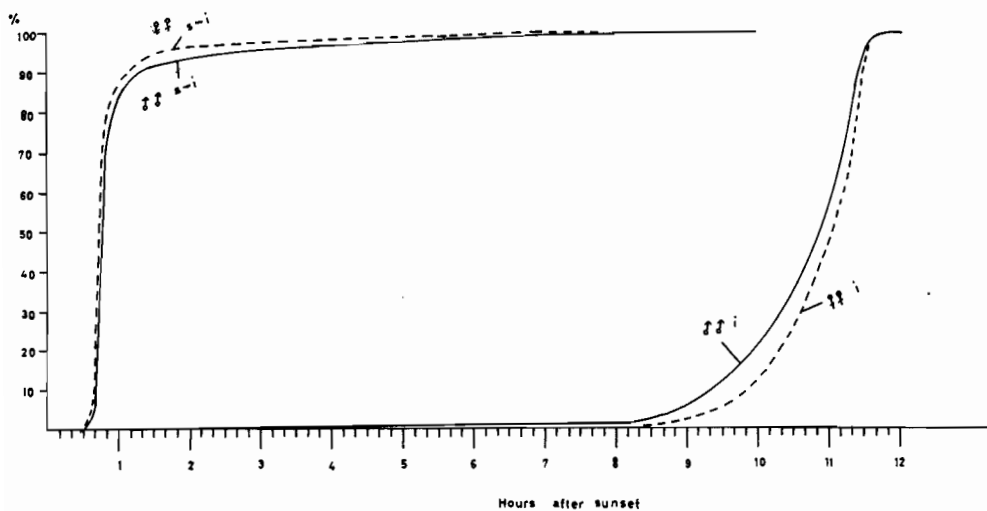


Fig. 1. Cumulative catches of *C. curtus* in percents of the total catch made during the last 45 nights in Year I. Ordinate: percent of a given sex and stage caught so far during the 45 nights. Abscissa: successive periods during the night.

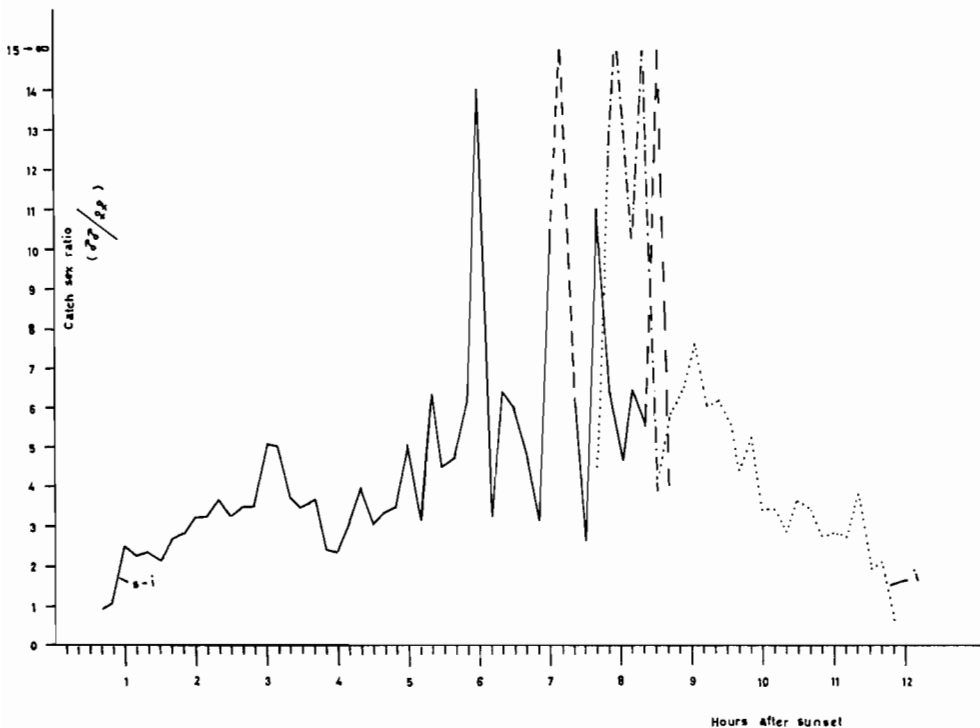


Fig. 2. Catch sex ratios for subimagines and imagines for the various catching periods of the night. The figure is based on the catches made during the last 45 nights in Year I and the catch sex ratios have only been calculated when the total catch of subimagines or imagines in the 45 identical catching periods exceeded 10 individuals. *Ordinate*: catch sex ratio, expressed as $\frac{\text{♂♂}}{\text{♀♀}}$. *Abscissa*: successive periods during the night.

before midnight were males.) The catch sex ratio of subimagines caught during the first hour after sunset in Year II was 1.97.

There are indications that the males need less time to complete moulting than do the females (TJØNNELAND, 1960). It is also noticed that the rise in the catches of male imagines after midnight starts sooner than the rise in the catches of female imagines. This has been shown in Fig. 1. The figure is based on the total number of male imagines and the total number of female imagines caught during the last 45 sampling night in Year I. In the figure the corresponding data have also been given for the subimagines.

By plotting the results in the form of cumulative percentages of the nights' total for each sex and stage, fluctuations resulting from small numbers of *C. curtus* caught in the middle of the night, are effectively smoothed (CORBET & TJØNNELAND, 1955). As far as the subimagines are concerned, the rise in the cumulative percentages is slightly higher for females than for males during the first part of the night. In the imagines the difference between cumulative percentages of the

sexes is more noticeable, especially during early morning. Here, the rise starts earlier in the males, the catches of females lagging somewhat behind in the beginning.

The differences are also brought out if the catch sex ratios — again expressed as $\delta\delta/\text{♀♀}$ — are plotted for the various 10-minutes' sampling intervals for the last 45 nights of Year I. This has been shown in Fig. 2. The catch sex ratios have only been calculated when the total number of insects caught in the sampling period exceeded 10 in the 45 nights.

In the catch sex ratio of the subimagines there is a general increase from sunset to midnight. Later in the night, when the catches of subimagines are small, there is a marked fluctuation in the catch sex ratios.

The catch sex ratio of the imagines fluctuates a good deal once the imagines first start to appear at the trap shortly after midnight. Later the catch sex ratio of the imagines shows a general, steady decrease towards sunrise.

For both imagines and subimagines, the tendency is the same as far as the catch sex ratio is concerned. In the middle of the night, the catches are small and the catch sex ratio fluctuates in a seemingly erratic fashion. For the remainder of the night, the general tendency is an increase in catch sex ratio with increasing crep values. (cf. NIELSEN, 1963 for the meaning of the term 'crep').

DISCUSSION

CORBET (1964) has discussed various methods employed for studying the emergence patterns of larvo-aquatic insects. In studying the emergence patterns of insects from Lake Victoria, comprehensive methods cannot be adopted. Little use has been made of representative methods — *e. g.* emergence traps — in these parts, the reason probably being the lack of manpower to operate a sufficient number of traps. Reliable quantitative information on the diel emergence pattern is accordingly lacking. Information on the emergence patterns has been obtained mainly by indirect methods.

In the case of *C. curtus* data obtained by light trap catches are adequate to determine the emergence pattern at Jinja. In dealing with *Ephemeroptera* the conclusion would be based on the nightly catches of subimagines, if these are caught by the trap. For species where the adult life span is short, as is the case with *C. curtus*, the conclusion may be no different if based on the catches of imagines only. In *C. curtus* there appears to be little overlap between subsequent emergence groups: few — if any — adults from one emergence group survive long enough to fly with the adults of the subsequent emergence group. Even if all the imagines caught during the first hour after sunset were assumed to be survivors from the preceding emergence group, they still represent only a small fraction of the imagines caught. Indeed, it is doubtful if all imagines caught during the first

catching hour of the night are survivors from an old emergence population. As previously mentioned, the highest catch of imagines taken during the first hour after sunset followed a day with very low air humidity and also a high day temperature. Although air humidity and temperature are not the only factors influencing survival, it seems unlikely that such a disproportionately large number should be able to survive such severe climatic conditions. It is more likely that these insects represent early emergers which, because of the high temperature, have moulted sufficiently early to fly shortly after sunset. It has already been demonstrated that there is a relation between the first catch of imagines and night temperature (cf. TJØNNELAND, 1960, Fig. 47). In the cited figure the left part applies to *C. curtus* males, and not females as stated. The right part of the figure deals with the females, as is evident from the text (cf. p. 26). Small captures of imagines have been seen in evenings following days with relatively low temperatures and a high relative humidity, and it is assumed that the imagines caught shortly after sunset are recruited partly from survivors, and partly from early emergers. The assumption is based on indications only. Longevity experiments carried out do not preclude that late emergers may survive to fly as imagines in the evening peak roughly 20–24 hours after emergence. Less importance should be attached to the fact that the evening catches of imagines show a high catch sex ratio, as the same is also true for the imagines caught shortly after midnight. The fact that the catches of imagines in the evening were higher (expressed as \bar{x}) in Year II than in Year I, while the total catches of imagines decreased from Year I to Year II, may also be an indication. It is clear that a light trap attracts the subimagines of *C. curtus*. Not all the subimagines attracted enter the trap. Some settle in the neighbourhood of the trap and remain settled till after they have moulted. If for some reason moulting is delayed — as may well be the case with late emergers — these insects are not ready to fly in the morning peak. Also, imagines which may have moulted in time, may be prevented from flying by severe climatic conditions. After sunrise, this part of the emergence group probably becomes flight inhibited for the whole day, and those which do survive the day are 'released into activity' after sunset the following evening.

When a light trap is run at the same site every night, an increase in the catches of survivors from the previous night may result. These survivors have been attracted to the trapping site the night before. If the trap is run at the same site every second night, or once a week as was the case during Year I, insects attracted to the site would, if they survived, disperse when released into activity the following night. There would thus be no 'concentration' of survivors at the site when the trap was run next time.

Although only one imago was caught during the first hour after sunset in Year I, there was a small, but steady, influx of imagines (all males) during the five following catching hours. Some of the insects caught were no doubt insects that had emerged and moulted early. The fact that no female imagines were

caught before midnight in Year I may well indicate that the imagines were derived from two different emergence populations. Some imagines may represent chance arrivals of scattered survivors from the night before.

As seen from Table 5 (p. 8) the catch sex ratio of the imagines exceeds the catch sex ratio of the subimagines, and this holds true for both years. The total catch of imagines thus contains fewer females in relation to the number of males than does the total catch of subimagines. This decrease could be brought about by several factors acting separately or together. If the emerging population were small, one could visualize the decrease being brought about by the females being more strongly attracted to the trap — or sampled from a wider area — than the males. This would again deplete the population of females more than the population of males early in the night and a small catch of female imagines would eventually result. Such an explanation cannot be accepted as the toll taken by the trap must be negligible.

The increase in catch sex ratio would also result if there was a difference in mortality during the period of quiescence and moulting, i. e. if the females showed the higher mortality. From the trap data it appears that the period of quiescence may well last slightly longer in the females (cf. Fig. 1, p. 8). To what extent a slightly longer quiescent period would lead to a heavier mortality can be debated. A number of factors, of which we know little, here enter into consideration, but the risk of dislodging would increase with a longer quiescent period. In the present case the difference in quiescent period between the sexes is probably not large enough to be of practical importance. But the possibility that the females may suffer a higher mortality during the actual moulting cannot be entirely ruled out.

Although mortality may well play a part, the explanation of the pronounced discrepancy in the catch sex ratios of subimagines and imagines must probably be sought elsewhere. If the flight activity figures of *C. curtus* are studied (cf. TJØNNELAND, 1960, Figs. 16a & 16b) it is noticed that the peak catches in the evening have occurred between 50—60 minutes after sunset whereas the peak catches in the morning have occurred between 30—40 minutes before sunrise. The evening and the morning peaks are therefore not symmetrically spaced about solar midnight. This may well reflect an asymmetry in the diel activity of this eocrepuscular insect. The discrepancies in the catch sex ratios previously described can then be explained by adopting CORBET's (1965) model explaining asymmetry in eocrepuscular diel periodicities of insects. (Fig. 3).

If the initiation of a sequence leading to activity starts at higher light intensities in the females than it does in the males, the discrepancy in catch sex ratios can be explained as follows. In the evening a light trap increases its efficiency from sunset till the end of the astronomical twilight. In the morning, the efficiency of a light trap decreases from the beginning of astronomical twilight till sunrise. In the evening it is likely that the efficiency of the trap increases slowly at first

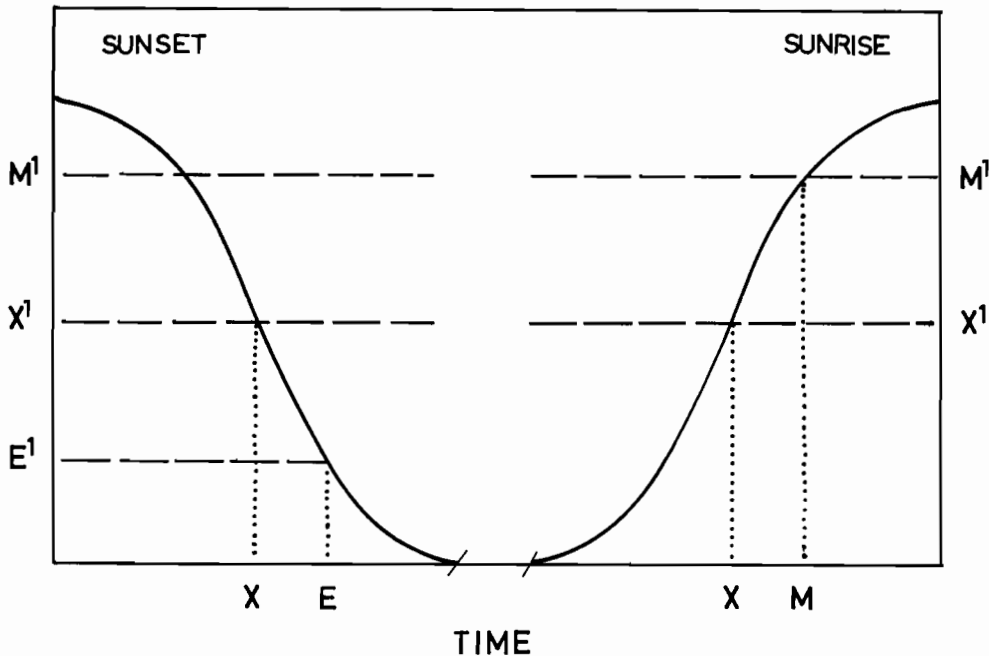


Fig. 3. CORBET's diagram illustrating the way in which a sunset activity peak (at time E) can fall at a lower light intensity than a sunrise peak (at time M). The activity sequence is released at time X (light intensity X^1). From CORBET (1965).

and indeed few insects have been caught during the first 10-minutes' catching periods. The efficiency of the trap then increases more rapidly to be slowed down towards the end of astronomical twilight. In the morning the efficiency of the trap is likely to decrease slowly at the onset of astronomical twilight; then follows a more rapid decrease which slows down as sunrise approaches.

If — in the evening — the initiation of the sequence leading to activity takes place at a higher light intensity in the females than in the males, the peak activity of females would precede the peak flight activity of males, provided the sequence leading to activity is of the same duration in the two sexes. The time lag between the female and the male activity peak may in the evening fall within a period where the trap is nearing its full efficiency, *i. e.* at a time when the efficiency of the trap changes little. Even so, the observed catch sex ratio must be assumed not to be the 'true' catch sex ratio, it will probably be slightly biased in favour of the males. By a 'true' catch sex ratio is not meant the true sex ratio of the subimagines or the imagines of which we know little.

If the initiation of the sequence leading to activity in the morning follows the same pattern, the activity peak of the females would fall later than the peak activity of the males. Here the time lag between the two may fall in a period where the trap is rapidly losing its efficiency, resulting in a pronounced increase in the

observed catch sex ratio for the imagines as compared with the observed catch sex ratio for the subimagines.

Such a time lag would seem to have a definite adaptive value, as the majority of females would start to fly after the males have started to swarm.

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CONCLUSIONS

It has been suggested that the \bar{x}/M_w ratio may be used as a rough and readily calculated index showing consistencies of catches by a light trap — provided either \bar{x} or M_w are also given. In the present case, the ratios for *Choroterpes curtus* (KIMMINS) are low, showing a low fluctuation of catches over a nine month observation period.

Imagines of *C. curtus* caught shortly after sunset are regarded as being a heterogeneous group recruited partly from 'survivors' from an older emergence group and early emergers from the last emergence group. It has also been pointed out that the running of a light trap at the same site every night may lead to an overrepresentation of survivors in the catches.

The dawn activity peak occurs at a higher light intensity than does the dusk peak in both sexes. As seen from Fig. 1, the dusk peak of the female subimagines slightly precedes that of the male subimagines. In the morning the dawn peak of the male imagines slightly precedes that of the female imagines. Provided the initiation of a sequence leading to activity takes place at a higher light intensity in the females than in the males, the asymmetry observed can be explained by adopting CORBET's (1965) model for asymmetry in ecrepuscular diel periodicities of insects.

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