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THE ADAPTIVE VALUE OF SYNCHRONOUS EMERGENCE IN THE TROPICAL AFRICAN MAYFLY POVILLA ADUSTA: A PRELIMINARY INVESTIGATION

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Abstract. From the study of a population of *Povilla adusta* displaying very marked lunar synchrony of emergence it has been estimated that such a population has an adaptive advantage over an asynchronous population of at least 8%. This has been estimated by determining the mean daily probability of survival of larvae and by determining the frequency during the lunar month of larvae competent to emerge. Since such larvae delay emergence until the second evening after full moon, the sum of the additional probabilities of death due to this delay can be calculated and is considered to be the inverse of a minimum value for the advantage of synchrony to the population.

Swarming, lunar periodicity, development

Povilla adusta Navas is a Polymitarcid mayfly widely distributed in tropical Africa. It displays a number of interesting and unusual features, among these being the wood-boring habits of the larvae, and the production, by the Malpighian tubules of the larvae, of a silk-like substance used to line the larval burrows (Hartland-Rowe 1958).

The most interesting feature of the species is that it displays a marked lunar periodicity of emergence in some of the lakes where it occurs (Hartland-Rowe 1955, 1958; Corbet et al. 1974; Bidwell 1979). Hartland-Rowe (1958) at Kaazi (32° 37′E, 0° 14′N) on Lake Victoria found that adults, which only live for about an hour, occur almost exclusively between 19.45 and 20.45 East African Standard Time, with most of the lunar month's emergence occurring on the second or third evening after full moon (Fig. 1). On these evenings the adults form large swarms and Table 1 shows the temporal distribution of such swarms in relation to the date of full moon. Table 2 (Fig. 2) shows the temporal distribution of adults collected at light at Jinja,

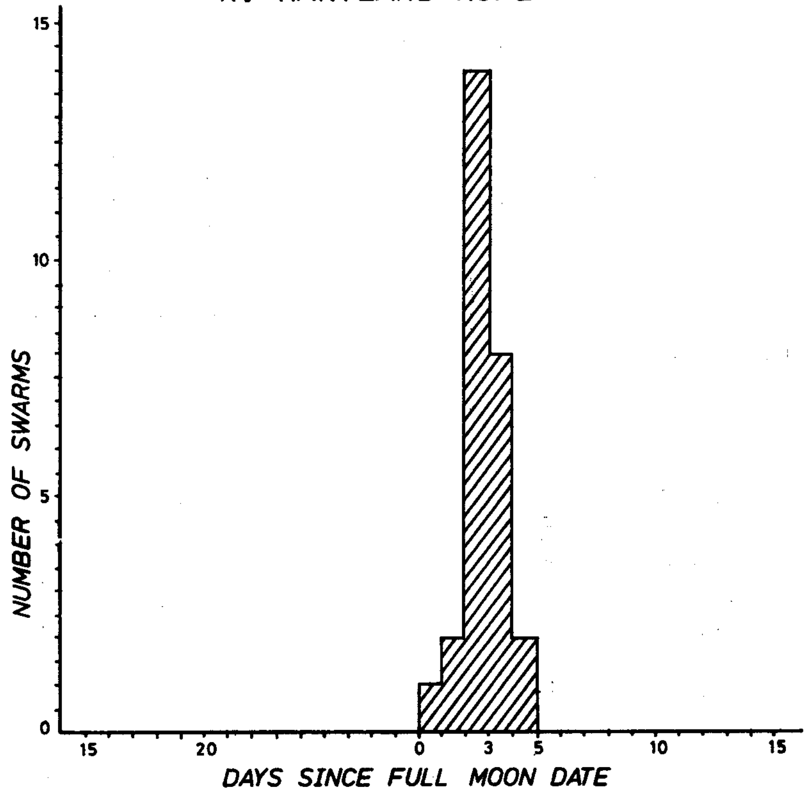

Fig. 1: Temporal distribution of Povilla swarms on Lake Victoria.

Uganda during three consecutive months. If there were no synchronisation with the lunar cycle, the expected proportion of individuals occurring on two nights would be about 6.7 %.

This highly synchronised emergence has several possible functions, including "swamping" asynchronous predation, or increased reproductive success. The object of the work described here is to determine the adaptive value of synchronous emergence to a population of *Povilla adusta* at Jinja, Uganda.

The theoretical basis for the study is to determine, from daily samples of larvae taken throughout the lunar month, (a) daily mortality rates and (b) the frequency of larvae competent to emerge. Because emergence is temporally restricted and predictable, the additional probability of larval death due to delay by competent larvae until the emergence date can be assessed. This additional probability of death is the inverse of the minimum adaptive value of synchrony to the population.

METHODS AND RESULTS

Samples of larvae were collected at Bugunga Swamp, Jinja, Uganda (33° 12.5'E, 00°25.5'N) under the supervision of Mr. Lucas Mwebaza-Ndawula. Owing to shortages of boats, motors, fuel and preservatives due to the war in Uganda the number and condition of samples was less than desired. However, there were sufficient to obtain size-frequency distributions for much of the lunar month. An eyepiece micrometer was used to measure head-width, the criterion of larval size.

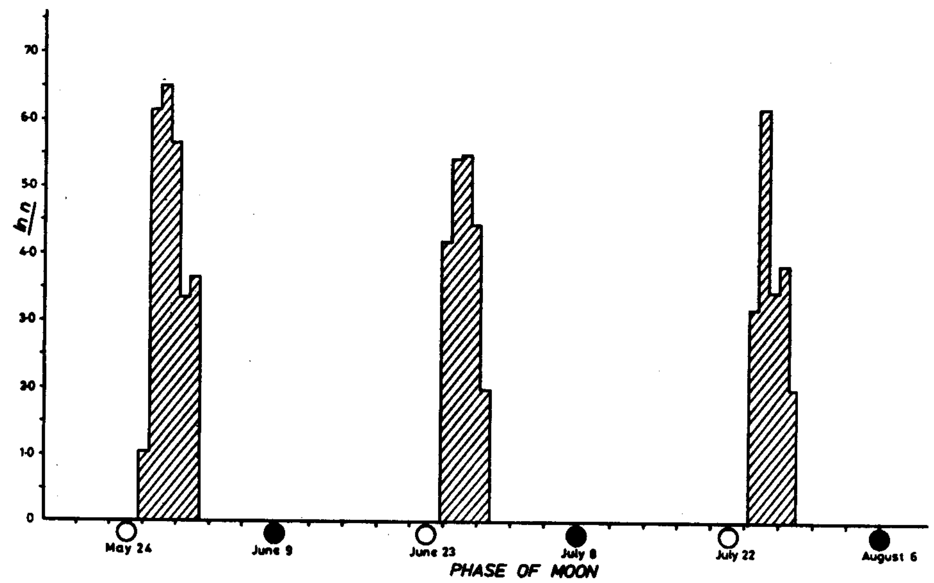

Fig. 2. Temporal distribution of adult Povilla adusta collected at light at Jinja, Uganda /data of P.S. Corbet/

The work of Corbet (1957) and personal observations made in 1956 show that the growth rates of larvae vary. So it is not surprising that the size-frequency distributions do not display distinct cohorts.

In order to convert the observed size-frequency data to age-frequency distributions it was assumed that Corbet (1957) is correct in concluding that the maximum duration of larval life is five lunar months. This figure, less two weeks to allow for the duration of the egg, is compatible with some growth data I obtained in 1956, and quoted in Corbet's paper.

A mean daily growth increment of 1.0164 is compatible with the size-frequency data and with a maximum larval life of four and a half lunar months.

Larvae whose head-width is over 1.1 mm can be sexed and it is noted that male larvae mature at a much smaller size than female larvae, as shown in Table 3.

Taken in conjuction with the mean daily growth increment of 1.0164, these figures suggest that male larvae will attain competence to emerge in $3\frac{1}{2}$ months, and females in $4\frac{1}{2}$ months.

The mean daily growth increment of 1.0164 was used to determine the mean ages of the size-classes observed as shown in Table 4.

It is observed that there is a decrease in frequency from size-class 1.0 - 1.3 to the maximum size-class 3.7 - 4.0. This decrease is nearly linear and the regression line of best fit (y - intercept: 198.6; slope -48.5) reveals a correlation coefficient of -0.973 between size and frequency (Fig. 3).

From this regression line the calculated mean daily probability of larval survival in size-class 1.0 - 1.3 (= age-class 56.3 - 72.5) and above is 0.98054.

Table 1. Dates of swarms of Povilla adusta observed on Lake Victoria in relation to the date of full moon.

Days after full moon	Number of swarms
0	1
1	2
2	14
3	8
4	2
5 - 29 summed	

Table 2. Temporal distribution of adult Povilla adusta collected at light by Dr.P.S.Corbet at Jinja, Uganda / 33° 12.5'E, 00°25.5'N/.

Month	Number captured on FM+2 and FM+3	Same, as percentage of the lunar month's total catch
June 1956	1169	87
July 1956	479	74
August 1956	534	87

Table 3. Head-widths /mm/ of competent male and female larvae

Male Headwidth	larvae Frequency	Female Headwidth	larvae Frequency	Female Headwidth	larvae Frequency
2.0	2	2.7	1	3.4	4
2.1	4	2.8	1	3.5	2
2.2	3	3.1	1	3.6	8
2.3	1	3.2	3	3.7	3
2.4	2	3.3	1	3.8	3
				3.9	2
Mean: 2.39 mm		Mean: 3.54 mm			

Table 4. Size-frequency and estimated age-frequency distributions of larvae.

Head-width /mm/	Estimated mean age /days/	Frequency
0.4-0.7	0.0- 34.4	9
0.7-1.0	34.4- 56.3	79
1.0-1.3	56.3- 72.5	157
1.3-1.6	72.5- 85.2	136
1.6-1.9	85.2- 95.8	127
1.9-2.2	95.8-105.8	105
2.2-2.5	104.8-112.7	75
2.5-2.8	112.7-119.6	65
2.8-3.1	119.6-125.9	68
3.1-3.4	125.9-131.6	46
3.4-3.7	131.6-136.8	53
3.7-4.0	136.8-141.5	13

Table 5. Probabilities of survival of male and female larvae which became competent to emerge before FM+2.

Days before FM +2	Percentage of month's emergence /A/	Probability of survival /P^n/ /B/	/A/x/B/
Males /n=12/			
27	0.083333	0.58825	0.04902
4	0.250	0.92440	0.23110
3	0.500	0.94275	0.47138
2	0.083333	0.96146	0.08012
1	0.083333	0.98054	0.08171
		Total:	0.91333
Females /n=31/			
29	0.03226	0.56558	0.01825
23	0.03226	0.63636	0.02053
21	0.06452	0.66187	0.04270
4	0.16129	0.92440	0.14910
3	0.25806	0.94275	0.24329
2	0.25806	0.96146	0.24811
1	0.19355	0.98054	0.18978
		Total:	0.91176

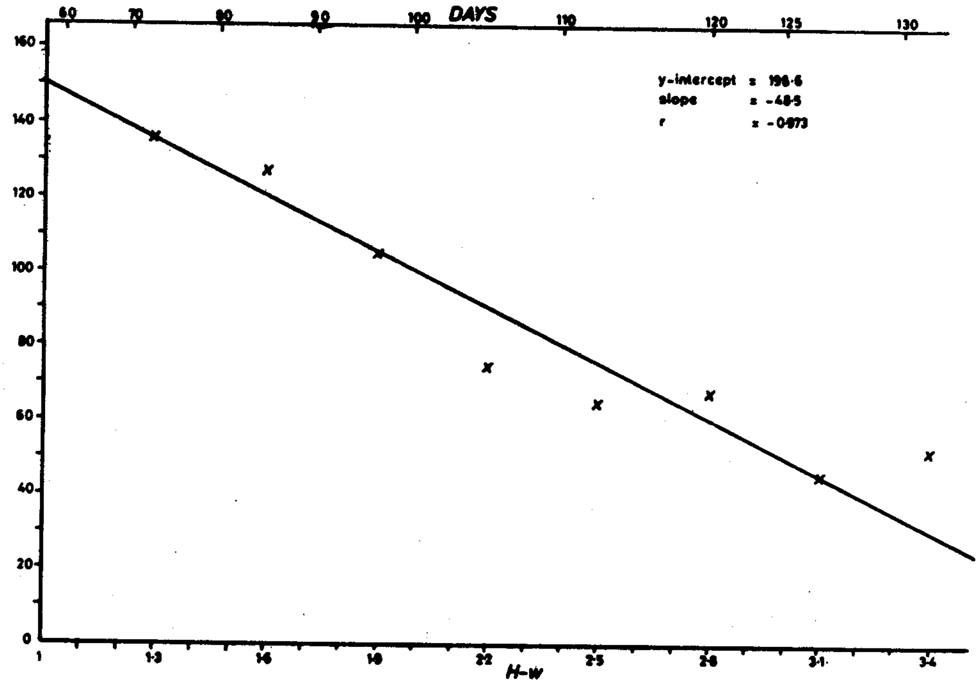

Fig. 3. Relationship between frequency and head-width /lower scale/ or mean age /upper scale/ of Povilla adusta larvae of head-width greater than 1.0 mm.

This figure can be used to assess the increased probability of larval death consequent upon the delayed emergence of larvae which become competent to emerge prior to the predictable date of emergence.

If the mean daily probability of survival is P, the probability of a larva surviving for n days is P^n.

Table 5 shows the probabilities of survival of those male and female larvae which became competent to emerge before the emergence date (FM + 2, the second evening after full moon). If every larva had become competent to emerge upon date FM + 2 the probability of survival until that date would have been 1.0. If all had become competent upon the previous day, the probability would have been 0.98054. The totals in the right-hand column shows the summed probabilities actually observed, so that the additional probability of death for the male larvae, for example, would have been 1.00000 - 0.91333 = 0.08667, and for the females 0.08824.

It is presumed that this additional probability of larval death is at least offset by a corresponding advantage to the population of synchronous emergence. That is to say, the synchronous population has an advantage over the asynchronous population of roughly 8 %.

DISCUSSION

Much more work is needed to refine the very preliminary data presented here. But these data suggest that the population under study may have an adaptive advantage of at least 8 % over an asynchronous population, implying that synchronous emergence is of major significance to the population.

Some populations of Povilla adusta do not display synchronous emergence. Corbet et al. (1974) reported that, of populations studied in five West African lakes, at least one showed a clear lunar periodicity of emergence, and at least one did not.

If the function of synchronous emergence is to increase the probability of reproductive success, asynchronous populations presumably lack it because their population densities are sufficiently high to ensure reproductive success without it. From the data presented in Table 2 it is estimated that this could only be true if the asynchronous population density were at least ten times as high as those of synchronous populations. Although no data are available, the extreme abundance of larvae observed at Kaazi and Jinja suggest that densities ten times as high are unlikely.

Another possibility is that the function of synchronous emergence is to "swamp" asynchronous predators. Perhaps asynchronous populations occur only in lakes where the intensity of predation is low. Clearly much more work is required, both to refine the data presented here, and to examine asynchronous populations of Povilla adusta.

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