PARTHENOGENESIS IN THE MAYFLY STENACRON INTERPUNCTATUM FRONTALE (BURKS) (EPHEMEROPTERA: HEPTAGENIIDAE)¹

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ABSTRACT: Development of unfertilized eggs of Stenacron interpunctatum frontale (Burks) is reported. Observed level of parthenogenetic egg development was 15.9% with hatching in 9.13%.

DESCRIPTORS: Stenacron interpunctatum frontale (Burks), parthenogenesis, mayfly, Heptageniidae, Ephemeroptera, reproduction.

The occurrence of parthenogenesis among mayflies has been confirmed for nine North American species. These include Ameletus ludens Needham (Clemens, 1922); Ephoron album (Say) (Britt, 1962); Stenomena interpunctatum (Say), Stenonema pulchellam (Walsh), Stenonema vicarium (Walker) (Huff and McCafferty, 1974); Baetisca rogersi Berner (Pescador and Peters, 1974); Stenonema femoratum (Say) (McCafferty and Huff, 1974); Hexagenia rigida McDunnough (Friesen and Flannagen, 1976) and Cloeon triangulifer McDunnough (Gibbs, 1977).

Additional North American species have been implicated as being potentially parthenogenetic on the basis of sex ratios observed in field collections. These species have been discussed by McCafferty and Huff (1974); however, experimental confirmations of parthenogenesis have yet to be demonstrated for them. European species showing parthenogenesis have been discussed by Degrange (1960).

The potential for parthenogenesis in Stenonema interpunctatum (Say) was first demonstrated by Huff and McCafferty (1974) when eclosion was produced from a single egg following a 32 day period of incubation. The total number of eggs incubated was not specified nor were further data reported for S. interpunctatum. The purpose of this paper is to report additional observations of parthenogenesis for this species³.

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³The genus Stenonema has been divided into two genera by Jensen (1974). The tripunctatum and vicarium species groups remain in Stenonema while the interpunctatum group now constitutes the genus Stenacron.

Methods and Materials

A series of nymphs of Stenacron interpunctatum frontale (Burks) was collected from Logan Brook at Route 158, approximately two miles east of Sherman Mills, Aroostook County, Maine, on August 3, 1976. The nymphs were transported in aerated gallon jars to the laboratory where cultures were maintained in an environmental chamber at a temperature of $72^{\circ} \pm 4^{\circ}F$ and a light-dark photoperiod of 16:8 hours.

As darkened wing pads became evident, each nymph was transferred to an individual plastic "ice cream" cup and further isolated in a cheese cloth covered rearing cage. A humidifier was used to maintain moisture at or above 60% saturation. Reared adults and associated stages were preserved in 70% ethanol.

Observations on parthenogenesis began on August 8 with the emergence of a solitary female subimago. The imaginal molt occurred the following day and after a period of isolation (24 hours), attempts were made to induce oviposition behavior by placing the imago in contact with a water surface. These efforts were unsuccessful and the imago was placed in a Petri dish containing a thin layer of distilled water in the event that oviposition might occur.

At the end of the next 48 hour period, oviposition had not occurred and the moribund imago was dissected. Recovered eggs were placed in a Petri dish containing distilled water and incubated in the environmental chamber.

Results

Observations on development are summarized in Table 1. Of 819 eggs recovered from the unmated imago, 89 hatched. An additional 66 eggs showed evidence of embryonic development but failed to hatch. The percentage of eggs that showed embryonic development was 15.9% and those hatching was 9.13%.

Table 1. Development of parthenogenetic eggs of S. i. frontale.

Development of Eggs	Number of Eggs Incubated	% of Total
no embryonic development	819	84.08
development without eclosion	66	6.77
development with eclosion	89	9.13
total	974	99.98

Observations of nymphal eclosion are presented in Figure 1. Hatching was first observed after 17 days of incubation and continued for 47 days. The greatest number of eclosions occurred on day 17 when 20 eggs hatched. Hatching declined thereafter until the final eclosion of a single nymph on day 47. Observations were terminated after 64 days without additional eclosion.

During the period of observation, a short series of adults was reared. Thirteen were female and five were male giving a sex ratio of 2.69 to 1.03.

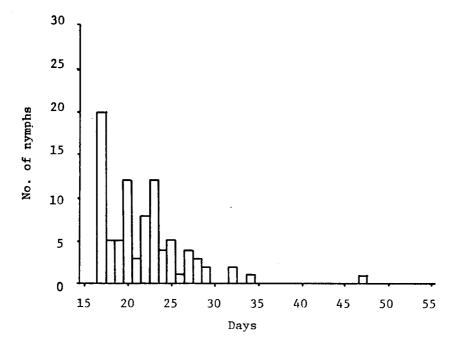


Figure 1. Days to eclosion of first instars of S. i. frontale.

Discussion

Obligatory parthenogenesis has been demonstrated for only a few species of mayflies (Clemens, 1922; Gibbs, 1977). These species typically exhibit very high levels of parthenogenesis and males are either extremely rare or unknown.

Faculative parthenogenesis is the more common form of parthenogenesis observed among mayflies and is found in species which normally reproduce sexually. Observed levels of parthenogenesis are typically low and arise from a

small proportion of naturally occurring diploid eggs which have failed to undergo meiosis (McCafferty and Huff, 1974). This type of parthenogenesis is expressed under natural conditions when a female is unable to locate a mate; thus the occurrence could be accurately referred to as occassional or accidental parthenogenesis.

In order for parthenogenesis to evolve, two conditions must be satisfied. The female must be able to lay eggs without mating, and a high proportion of those eggs must hatch (Soumalainen, 1962). It has been clearly shown that the potential for parthenogenesis does exist in *S.i. frontale*, however it is not known if this potential is realized under natural conditions.

Several authors (Gibbs, 1977; McCafferty and Huff, 1974; Degrange, 1960) have observed that females of various species would readily oviposit when placed in contact with a water surface. Degrange (1960) also observed that some species could not be induced to oviposit by this method and concluded that some particular pre-oviposition activity such as a flight period was essential. It was further suggested that the muscular activity associated with flight promoted the passage of eggs through the oviducts and permitted their expulsion.

Dissection of several reared female imagos revealed that eggs had not entered the oviducts. Since the small size of the rearing cages severely hampered flight activity, an extended period of flight may be required for oviposition to occur in S.i. frontale. This might also explain the failure of the imago to oviposit when placed in contact with the water surface.

The advantages associated with obligatory parthenogenesis have been briefly reviewed by Gibbs (1977). Tjonneland (1970) and Gibbs (1977) also discussed the potential effects of obligatory parthenogenesis upon flight activity and emergence patterns.

The advantages of faculative parthenogenesis do not appear to have been investigated for mayflies. Faculative parthenogenesis may function as a means of continuing a genetic line in the event that a mate cannot be located, however, it would seem that reported levels of parthenogenesis (normally less than 10%) are too low to be of significance in the population dynamics of the species. McCafferty and Huff (1974) have suggested that the low levels they observed may represent a rudimentary type of parthenogenesis. Soumalainen (1960) has suggested that low levels may represent a transitional stage between sexual reproduction and thelytokous (female producing) parthenogenesis.

Due to the presence of males and presumably sexual reproduction, it is concluded that parthenogenesis in S.i. frontale is faculative and deuter-otokous (producing both sexes). However, the actual type of parthenogenesis can only be verified by rearing successive generations in order to determine the sex ratio of the resulting nymphs. Until this is accomplished, it is possible

that parthenogenesis as observed in S.i. frontale is thelytokous and that males are produced only through normal sexual reproduction. Similarly the mode of parthenogenesis, whether apomictic (ameiotic) or automictic (meiotic), can only be determined through cyto-genetic investigations.

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