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Swarm Behavior of Hexagenia atrocaudata in Relation to Temperature and Relative Humidity (Ephermeroptera)

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INTRODUCTION

In a previous paper ¹ an attempt was made to record the swarming phenomena manifested in the behavior of *Stenonema* vicarium at sundown over the banks of Darby Creek near Clifton Heights, Pennsylvania. In a later publication,² observations were made on *Isonychia christina* maneuvering at a high altitude a short distance from the same location. As a result of these observations it was reasonable to conclude that a more intensive and thorough study of such behavior patterns would be of interest. Possibly, also, these patterns might be correlated in some degree with genetic relationships.

METHODS

The methods used during both nymphal and imaginal surveys involved a close analysis of the area in order to determine any change occurring among the population. Reluctantly, it was found that the best time for collecting adults in numbers was about 9 o'clock P.M. (E.S.T.), at which time the insects would be circling vigorously about electric lights on the banks of the stream in a nightly performance that lasted for thirty minutes,

¹ COOKE, HERMAN G., 1940. Observation on mating flights of mayflies, *Stenonema vicarium*. ENT. NEWS, 51: 12.

² COOKE, HERMAN G., 1942. Mating flights of *Isonychia* mayflies (Ephemeroptera). ENT. NEWS, 53: 249.

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after which the insects vanished. Observations throughout the night revealed only scattered individuals returning at random.

The duration of these performances paralleled those indicated for normal flights, but differed widely both in the absence of those graceful movements and in the attempts to copulate that so strikingly characterize active mating. Each summer both nymphal and imaginal collections contained members of the three genera known in the area, namely, *Stenonema, Isonychia*, and *Cloeon*.

The methods used in determining the amplitude of rhythmic movements and their height above the surface of the land or water were as follows: (1) Tags were tacked at known levels on wooden strips that were placed vertically in or beside the stream and allowed to project above the surface of the water or ground over which the maneuvering took place; (2) rolls of tape with tags attached at measured intervals were suspended from the upper branches of trees or nearby shrubs to the water or ground beneath. The average distance reached by the insects while ascending and descending was plotted by reference to these devices.

During observations on flight behavior, it became apparent that the occurrence of swarming depended also upon weather conditions. Since almost nightly visits were made to Darby Creek and records kept, it is possible to study activity with relation to the temperature and humidity records of the weather bureau.

Observations on Temperature

Beginning July 27th, 1942, all searches were temporarily suspended because of a period of heavy rainfall (two inches of rain fell within a thirty minute period) accompanied by high winds lasting for several days. Then, on August 8th, 1942, it was observed that the entire area had been invaded by countless numbers of *Hexagenia* imagines. Although the source of these newcomers was uncertain, nevertheless, advantage was taken of their presence for the purpose of investigating the nature of their swarming behavior.

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On August 23rd, at 7:30 P.M., as the thermometer registered 72° F., flight movements were observed over a wide area. On the following two days there was a sharp fall to 64°, and flight activities ceased. This temperature proved to be unfavorable both for swarning and for nymphal emergence in this and in related genera. At the same hour on the 26th, at a temperature

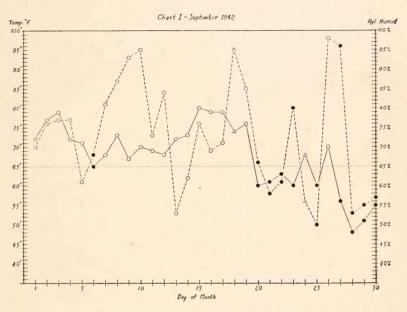


Fig. 1. Records for September 1942. Solid line is temperature; broken line is relative humidity; $\circ =$ activity observed; $\bullet =$ no activity; $\otimes =$ no record; $\triangle =$ rain.

four degrees higher, activity was resumed. This incident revealed the limiting effect of temperature upon the activities of these insects even during the month of their greatest abundance.

The following table gives the temperature and humidity data ³ for a part of the period under discussion.

³ Records of relative humidity and temperature were obtained through the courtesy of the U. S. Weather Burcau at Philadelphia, Pennsylvania. All readings are given at 7:30 P.M., Eastern Standard Time.

Dates	Relative Humidity	Temperature	Activity Observed
August 22nd, 1942	74%	80°	Activity
August 23rd, 1942	92%	72°	Activity
August 24th, 1942	57%	64°	No activity
August 25th, 1942	52%	68°	No activity
August 26th, 1942	58%	68°	Activity
August 27th, 1942	59%	68°	Activity
August 28th, 1942	70%	72°	Activity

The dependence of swarming on environmental conditions is further documented by the detailed comparison that appears on the two graphs (figs. 1 and 2). These graphs represent weather bureau data for September 1942 and 1943 together with the

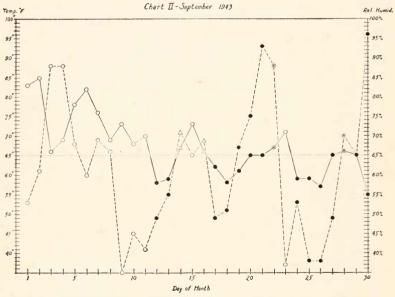


Fig. 2. Records for September 1943. Symbols are the same as in fig. 1.

daily records on flight activity. Temperature and humidity are both represented, by a solid and a broken line respectively, and are plotted against the days of the month. The 65° temperature level is indicated by a dotted line, for at temperatures below this no activity was ever observed by the writer. Attention is called to those days that show a sudden drop in temperature correlated with absence of activity, for example, on September 12th, 1943, when the temperature registered 58° , 12° lower than on the day before. During the remaining days of the month, except the 15th and 23rd, which were recorded at 73° and 71° F., respectively, the temperature maintained a constant low level, thus causing all flight movements to be discontinued. The humidity difference, however, does not appear to represent a limiting factor as regards the aerial performances of these insects.

Observations on Swarming Maneuvers

The observations for 1943 were made on a series of companies of *Hexagenia atrocaudata* swarming over the stream near the same locality as in the previous year. The performances began well after sundown and lasted until fully covered by darkness.

Copulation was observed in several instances and took place in a manner strikingly similar to that found in other genera of this order.

The following detailed observations on the swarming or mating-flight were made about 7:00 P.M., August 9th, 1943.

The individuals ascended to about fifteen feet above the water and then descended in an almost vertical power dive to about eighteen inches from its surface. At this point they pulled upward again and forward to a horizontal position, from whence they again descended. These movements were repeated over and over until darkness intervened.

As regards the flights occurring over the land, these were, for the most part, far more compact than those conducted over the stream. They were of shorter duration and were executed in a series of vertical zigzag-like movements, describing 45° angles, in rapid succession. At the height of the performance the individuals showed a high nervous tension with only feeble attempts toward copulation. Near the end of activity, the swarm apparently reached such a state of flux and disorder that the failure of individuals to avoid capture was far more noticeable than their attempts to elude the net; a tendency so unlike that

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observed in *Isonychia*, which I found very net-shy, or in *Callibaetis*, which Needham⁴ records as among the most wary forms.

Discussion

Clemens ⁵ and Murphy ⁶ have already recorded that low temperatures inhibit activity. My own observations, as recorded in detail above, also indicate cessation of activity below 65° F. Although the records are for *Hexagenia* the essential facts involved are also manifested in the behavior of *Isonychia*. As regards the possible influence of humidity, no definite conclusions are drawn.

The movements in the mating flight of *Hexagenia* are characteristic and peculiar and readily distinguishable from those of *Stenonema* and *Isonychia*. They appear to differ also from the movements of other genera as described in the literature by Needham and other writers.

Although they had not been found in the preceding years, during the two years of this study, 1942 and 1943, members of H. atrocaudata were quite numerous. During August of the following year, 1944, the swarm became so greatly reduced that only small companies could be encountered under the most favorable condition, and, finally, by the summer of 1945, flight movements became completely suspended. The decline and disappearance of this species during certain seasons remains one of the most baffling mysteries of my ephmeridal investigations in this area.

In a recent report on the emergence and flight movement of the species of *Hexagenia*, Lyman⁷ observed that wind direction aided in the distribution of sub-imagines and imagines while in flight. He also advanced the theory, supported by Langlois,

⁴ NEEDHAM, J. G., JAY R. TRAVER, and YIN-CHI HAU, 1935. The biology of the mayflies. P. 10.

⁵ CLEMENS, W. A., 1917. An ecological study of the mayfly Chirotenetes. University of Toronto Studies Biol. Ser. 17.

⁶ MURPHY, HELEN, 1922. Notes on the biology of the mayflies genus *Baetis*. Bull. Lloyd Library, Ent. Ser. 2.

⁷ LYMAN, EARL F., 1944. Emergence, swarming and mating in *Hexagenia*. ENT. NEWS, 55: 207-210.

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that the difference in emergence for alternating years indicated a cyclic trend in the population of *Hexagenia*.

Because of the very nature of the rocky stream-bed over which my own surveys have been constantly conducted, it seems that only with the greatest difficulty could the immature stage of *Hexagenia atrocaudata* have survived without having been previously encountered.

The writer wishes to acknowledge his gratitude to Dr. Philip P. Calvert, of the University of Pennsylvania and the Academy of Natural Sciences, for his stimulating interest freely shown during the course of this study. Thanks are also due Mr. Howard Levy of City College, New York City, graduate student of Dr. H. Spieth, for confirming the classification of the species here involved.

Odonata of Voyages under the Auspices of the New York Zoological Society

By PHILIP P. CALVERT, Cheyney, Penna.

When sending me Odonata collected at the Tropical Research Station of the New York Zoological Society at Kartabo, British Guiana,¹ Dr. William Beebe, Director of the Station, sent also some Odonata collected on various voyages made under the auspices of the Society. These are listed below with a few comments.

I. VOYAGES OF THE STEAM YACHTS Noma, 1923, AND Arcturus, 1925, to the Galápagos

Indefatigable Island, Seymour Bay, April 22, 1923: Pantala flavescens (Fabricius), one male.

South Seymour Island, April 23, 1923: *P. flavescens*, three males.

Hood Island, Lake, 27.IV.1925: Tramea (Trapezostigma) cophysa darwini Kirby, one male.

¹ These are reported on in a paper to be published in Zoologica, the Society's journal.