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Adult Life and Emergence of *Dolania americana* in Northwestern Florida (Ephemeroptera: Behningiidae)

Abstract

The adult habits and emergence of *Dolania americana* (Ephemeroptera: Behningiidae) were studied at the Blackwater River in Northwestern Florida. The adult life is crepuscular, beginning about 1½ hrs before sunrise with emergence of male subimagos. Males molt to imagos, female subimagos emerge, males and females mate, and females begin to oviposit in a fairly precise time sequence over the following hour. Only a few adults survive past sunrise. Females never molt to imagos and are polymorphic. Emergence is seasonal and begins between the end of April and the middle of May, depending on climatic conditions. Emergence is photoperiodically entrained. Water temperature is a phase setter and light intensity acts as a synchronizer.

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1. Introduction

The family Behningiidae (Ephemeroptera) is composed of three genera whose members are among the least known mayflies in the world. The family was first found by BEHNING (1924) who discussed two nymphs as "nov. gen., nov. sp.?" from the Volga River at Mychkine above Rybinsk, European R.S.F.S.R. ULMER (1924) redescribed these nymphs but did not name them. Later LESTAGE (1929) established *Behningia* and named the Volga River species *B. ulmeri*.

The first description of a male imago was given by TSHERNOVA (1938) who described nymphs and adults of *B. ulmeri* (?) from the lower Amur River, Far Eastern R.S.F.S.R. EDMUNDS and TRAYER (1959) later named the Amur River specimens as a new species, *B. tshernovae*.

MOTAŞ and BĂCESCO (1937) described *B. lestagei* from nymphs collected in the Dniestre River, now in Moldavian S.S.R., and later gave a further description of the species (MOTAŞ and BĂCESCO,

1940). KEFFERMÜLLER (1957) discovered *B. lestagei* in the Warta River, Poland. In 1959, KEFFERMÜLLER described the male and female adults of the species and, in 1963, she described its unique habits. KEFFERMÜLLER (1959) assigned the Warta River specimens to *B. lestagei* on the basis of published descriptions, but suggested that an examination of types might show *B. lestagei* to be a synonym of *B. ulmeri*.

The family Behningiidae was originally proposed by MOTAŞ and BĂCESCO (1937) and later by TSHERNOVA (1938). There has been some question concerning the date of the paper by MOTAŞ and BĂCESCO (EDMUNDS and TRAVER, 1959), but Prof. Dr. MOTAŞ assures us that the paper establishing Behningiidae was published in 1937 (personal communication). LESTAGE (1938) synonymized the family by placing *Behningia* in the Oligoneuriidae; however, MOTAŞ and BĂCESCO (1940) placed the genus in a separate monotypic subfamily of the Oligoneuriidae. DEMOULIN (1952) restored the group to family status. EDMUNDS and TRAVER (1959) placed Behningiidae in the superfamily Ephemeroidea, a placement confirmed by TSHERNOVA (1970), EDMUNDS (1972), LANDA (1973), RIEK (1973), and McCAFFERTY (1975).

EDMUNDS and TRAVER (1959) established *Dolania* for the species *D. americana* from the Savannah River and its tributaries, South Carolina, from four nymphs collected by T. DOLAN. Biological notes by Mr. DOLAN were included. SCHNEIDER (1967) recorded nymphs of *D. americana* from northwest Florida and, the same year, we also discovered *D. americana* to be common in the shifting sand bottom rivers of north-west Florida.

TSHERNOVA in TSHERNOVA and BAJKOVA (1960) established *Protobehningia* for the species *P. asiatica* which was collected from the lower Ussuri River, Far Eastern R.S.F.S.R. Only three nymphal specimens of the species are known.

The nymphs of all three genera live in clean shifting sand rivers. KEFFERMÜLLER (1959) discussed the burrowing habits and ecology of *Behningia lestagei* and TSHERNOVA and BAJKOVA (1960) suggested that *Protobehningia* was also a sand burrower because its nymph shares several morphological characters with *Behningia* and *Dolania*. Research on nymphal ecology and habits of *D. americana* indicate its habits are very similar to those of *Behningia* (PETERS and JONES, 1973, McCAFFERTY, 1975, and unpublished data).

The adult behavior of only *Behningia lestagei* has been described (KEFFERMÜLLER, 1963). Since discovering *Dolania americana* in Florida, we have been studying its emergence and adult behavior. This report gives our results to date.

2. Description of Study Area

Studies on *Dolania americana* were conducted at the Blackwater River, Okaloosa and Santa Rosa Counties, Northwestern Florida. Following the river classification of PENNAK (1971), the Blackwater is a permanent river of moderate width, slow to moderate current, and sand substrate. The sand is mostly fine to coarse in texture (.105–1.0 mm in diameter) with the medium particle size (.25–.50 mm) predominant. Summer maximum water temperatures fall below 30 °C and winter minimums are above 10 °C. The water is soft, slightly acidic, exceptionally clear, and carries very small quantities of organic and inorganic matter, with no apparent organic pollution. It flows through forests and supports a restricted crop of rooted aquatic plants. Detailed discharge data and water chemistry analyses are published by the U.S. Department of Interior Geological Survey (1975 and previous years). Geological, physical, and chemical aspects of the river were given by W. BECK (1973) while biological and historical aspects were discussed by PETERS and JONES (1973).

A visitor to the river first notices the large bars of clean, shifting sand along the river. Streams and rivers with shifting sand bottoms are widespread within the

Southeastern Coastal Plains; however, many are disturbed and the sand is biologically unproductive. The Blackwater River is still in a natural state for almost its entire length and the shifting sand bottom is biologically productive. Along with *D. americana*, nymphs of *Pseudiron meridionalis* TRAVER, *Homoeoneuria dolani* EDMUNDS, BERNER and TRAVER, *Progomphus obscurus* (RAMBUR) and larvae of

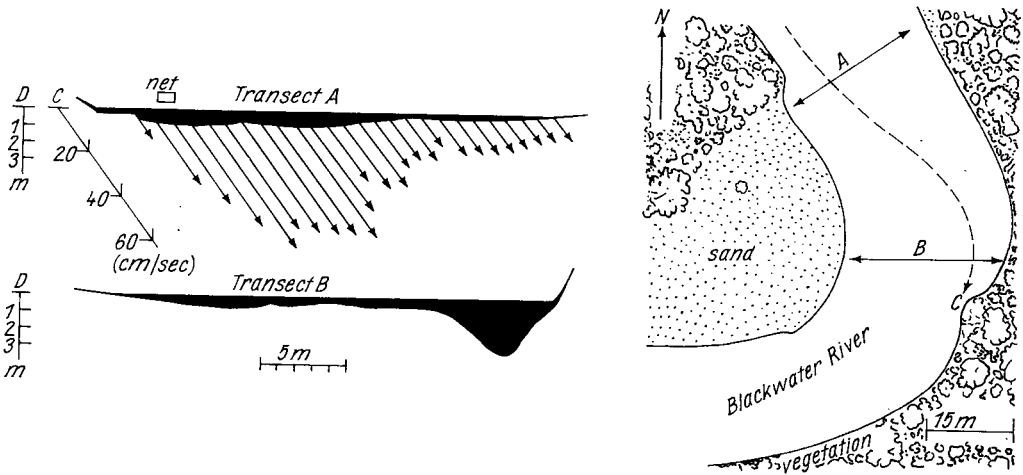


Fig. 1. Blackwater River at riverside study site with transect showing surface current speed and position of surface drift net. Abbreviations: A, B position of transects; C current; D depth (data taken 22–23-V-73, river about 35 cm below mean depth).

Paracladopelma sp. and "*Parachironomus*" *demeijeria* (KRUSEMAN) can be found in the clean, white, shifting sand.

Most studies were conducted at the riverside site of the Florida A & M University Biological Station, 5 km NW of Holt. Figure 1 shows the river and sand banks at this research site. Unless otherwise stated, all data were taken from this site.

Some data is included from Kennedy Bridge on the Blackwater River, 12 km W of Blackman and 42 river-km upstream from the riverside site. Other agencies have contributed data on the Blackwater River and the climate in Northwestern Florida. Full sources are given now, but abbreviations will be used in the rest of this paper:

Coldwater Tower, DOF. — Coldwater Tower, District 1 of the Division of Forestry, Florida Department of Agriculture and Consumer Services, 15 km W of the study site, supplied daily temperature records (taken at 1300 hrs) and rainfall data for the entire period of study. From January 1975 to date, daily records also include minimum and maximum air temperatures.

Jay Experiment Station, NOAA. — The Environmental Data Service of the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce supplied complete air temperature and rainfall records for the period of study taken from the Florida Agricultural Experiment Stations of the University of Florida, Jay, N of Milton and 35 km NW of the study site.

Highway 4, USGS. — The Water Resources Division of the Geological Survey, U.S. Department of Interior, provided daily discharge data on the Blackwater River taken at the point where the river crosses Florida State Highway 4, W of Baker and 23 river-km upstream from the study site.

It was with the generous cooperation of these agencies that we prepared Figure 2 which shows discharge on the Blackwater River and general climate patterns in Northwestern Florida over the entire life cycles of the three generations of *Dolania americana* studied. A few comments are necessary. We used temperature data from the Jay Station (supplied by NOAA) because this was the nearest location with complete records for the entire study period. Average monthly

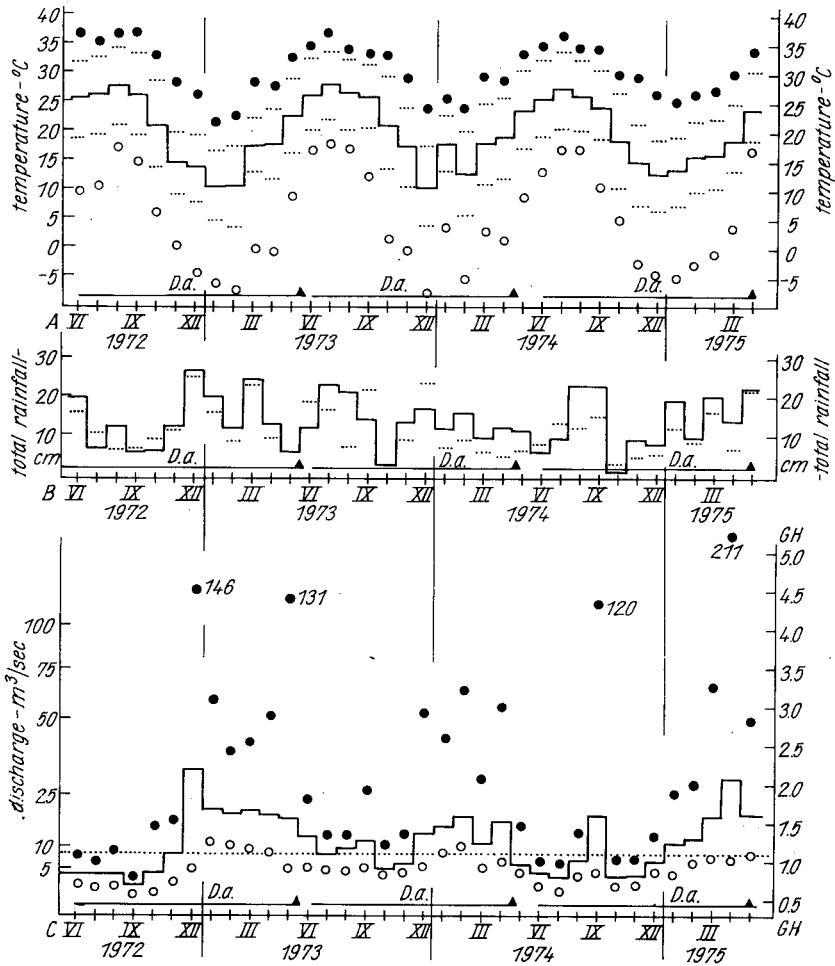


Fig. 2. Seasonal climate in Northwestern Florida over life cycles of 3 generations of *Dolania americana* (*D. a.*) studied. *A.* Air temperatures: solid line = average monthly temperature; dotted lines = average monthly minimum or maximum temperature; dots = record low or high temperature for month (data from Jay Exp. Stn., NOAA). *B.* Total monthly rainfall: solid line = data from Jay Exp. Stn. (NOAA); dotted line = data from Coldwater Tower (DOF). *C.* Discharge of Blackwater River at Highway 4 (data from USGS): solid line = average monthly daily mean discharge; dots = minimum or maximum daily mean discharge for month; GH = gauge height in metres; dotted line = 22-year mean.

temperatures from Coldwater Tower (DOF) in 1975 are 0.4°C lower than average monthly temperatures in Jay, while monthly high and low temperatures are $1\text{--}2^{\circ}\text{C}$ more extreme at Coldwater than at Jay. Thus we believe that Figure 2*A* gives an accurate picture of seasonal air temperatures. Rainfall totals are included for both of these stations, as rainfall at any one point in Northwestern Florida can be very localized and sporadic. The line drawn at $8.4\text{ m}^3/\text{sec}$ in Figure 2*C* represents the mean discharge computed by the USGS after 22 years. After 24 years, mean discharge rose to $8.7\text{ m}^3/\text{sec}$, but we have kept the same level in Figures 5–8 as this represented an increase in gauge height of only about 2 cm. Mean discharge is slightly misleading, because the flow maximums (up to $741\text{ m}^3/\text{sec}$) are much more extreme than the flow minimum ($1.7\text{ m}^3/\text{sec}$). Actually, flow duration data computed on the Blackwater River from 1951–1972 indicated that daily discharge would be between $1.7\text{ m}^3/\text{sec}$ and $8.5\text{ m}^3/\text{sec}$ 73% of the time.

Gauge height at Highway 4 (USGS) is indicated in Figure 2C. The gauge is set in a deep point in the river. From information collected in making the two transects in Figure 1, a gauge height of 1.11–1.13 m (at mean discharge at Highway 4) will equal an average depth of 97.5–99.5 cm at the riverside site. Average depth was calculated as the average of the mean depth of the two transects, and assumes that the shifting sand bottom does not move. Further reference to depth in this paper will be given in centimeters above or below mean depth. We should also mention that discharge at the study site is greater, because of intervening tributaries, than discharge at Highway 4.

3. Methods

a) General

Emergence and behavior of *Dolania americana* adults were observed closely in 1973, 1974, and 1975, and daily data were taken for: air and water temperatures, relative humidity, barometric pressure, moon phase, moon visibility, wind, weather conditions, river depth, and light. We occasionally refer to emergences from 1969–1972 when this information supplements 1973–1975 data, but regular observations did not begin until 1973.

Since relative humidity, measured by a sling psychrometer, always exceeded 90% in pre-dawn hours, these readings were discontinued after 1973. Wind, when present, was recorded with a hand-held Dwyer wind meter. Rainfall, cloud cover, moon visibility, and general weather conditions were observed and recorded.

Air and water temperatures were taken before and during emergence with a Webster pocket thermometer (-30°C to $+50^{\circ}\text{C}$ in 1°C increments) 5 cm below the surface of the river. This thermometer was compared with a standard Fisher thermometer (54 – 272 , -1°C to $+51^{\circ}\text{C}$ in 0.1°C increments). Between 17°C and 19.5°C , the Webster pocket thermometer recorded an average of 0.2°C below the Fisher thermometer. Daily maximum air and water temperatures were recorded on Taylor minimum-maximum thermometers, one placed in the river under a shaded bank and the other away from the river under trees. Temperatures from minimum-maximum thermometers were not standardized, as these thermometers were stolen occasionally and had to be replaced during the course of the study.

Data from Coldwater Tower (DOF) are given in Central Standard Time. All other times given in discussing the emergence of *Dolania* are standard time, although usually converted to time before sunrise. Sunrise, moonrise, moonset, and moon phase were taken or calculated from the American Ephemeris and Nautical Almanac (U.S. Naval Observatory) for the appropriate year according to methods described in the 1946 Supplement to this publication. Latitude and longitude for the riverside site are $30^{\circ}44' \text{N}$, $86^{\circ}47' \text{W}$.

River depth was measured on marked wooden poles. These measurements were converted into centimetres above or below mean depth by standardization against the gauge at Highway 4 on days when the river was near mean depth.

Light readings were taken with a Salford Electrical Instruments Exposure Photometer in 1973 and 1974. Readings of total visual light were expressed as log foot lamberts and later converted into lux. This meter could not record light below a level of .034 lux, so a new meter with a lower range of light sensitivity was used in 1975. This was a portable photometer/radiometer with a silicon cell detector head made by Gamma Scientific Inc. (models 900 and 820-30L respectively) and gave readings directly in lux. All 3 years, readings were taken just above the horizon to the northeast at approximately the point where rays of sunlight were first visible.

Different combinations of lights were used to attract adults of *Dolania*, including a mercury vapor bulb powered by a portable electric generator, hand-held and head-mounted flashlights, as well as an 8-watt cool white fluorescent bulb and an 8-watt black light (ultraviolet) fluorescent bulb, both powered by portable battery packs. These last two lights were used most frequently and are those referred to in Tables 2 and 5. Other collections of *Dolania* adults were made with sweep nets and by picking up adults floating on the river or lying on the sand banks.

b) Surface drift

Surface drift was sampled regularly. Drift nets were rectangular, $1 \text{ m} \times 18 \text{ cm}$, mounted on a float so as to collect only the top 5 cm of surface drift. The float was tied by rope to a bush and pushed out over a channel about 5 m into the river with an aluminum pole to the position indicated

in Figure 1. The river was about 30 m wide at this point, so the surface net sampled some 3% of a river cross section (transect A, Fig. 1). Current speeds were measured just below the surface at 1 m intervals across transect A (Fig. 1) with an InterOcean flowmeter (TSK-USA model 313). From these figures we can estimate that the drift net sampled approximately 5% of the surface current flowing past this point in the river. As measurements used to prepare Figure 1 were made when the river was below mean depth, the percentages of total surface drift sampled by the nets will be slightly less as the river level rises. Netting was a coarse mesh nylon (mesh opening about 2.5 mm). Nets were changed at 15 min intervals from 2 hrs before sunrise to 15 min after sunrise, although on a few days sampling started 15–30 min later. On the rainy morning of 4 May 1975 nets were changed irregularly between storms so that only a total exuvia count is

Table 1. Surface drift samples of emerging *Dolania americana* for 30 April 1975. Samples were collected every 15 min from 2 hrs before to 1 hr after sunrise (sunrise at 0605 hrs), but cumulative percentages were only figured for the 2¼ hr period used to compare relative size of all emergences

Time	Numbers Collected			Exuviae	
	♂	♀ Morphs Light	Dark	No.	Cumulative % Totals
0420	0	0	0	1	<.1
0435	0	0	0	2	.2
0450	1 ¹	0	0	14	1.1
0505	6	0	0	307 ²	21.4
0520	15	1	1	159	31.9
0535	49	20	0	187 ²	44.3
0550	78	164	3	476	75.7
0605	41	98	2	252	92.3
0620	11	15	0	116	100.0
0635	6	3	0	59	
0650	2	4	0	54	
0705	3	0	0	36	
<hr/>					
Totals-Sunrise + 15 min	201	298	6	1514	
<hr/>					
Totals-Sunrise + 1 hr	212	305	6	1663	

¹ Male subimago in process of molting.

² Dead male nymph – not counted.

possible. About 1 min of each sample was lost during the time the nets were changed. Samples were individually counted to obtain data for each day similar to that presented in Table 1 for one date, and samples were preserved in 90% alcohol. When the emergence was large, samples were sometimes continued until 1 hr after sunrise (Table 1 as an example). Since sampling after sunrise showed a continuous decline in numbers, only the totals of exuviae through the 15 min sample following sunrise were used to quantitatively compare relative emergence size. On a few dates, the exuvia counts (to be given in Figs. 5–7) had to be estimated:

13 May 1973, 358 exuviae. – We do not have an exuvia collection for this date. There were 86 adults collected in the surface drift. In other collections involving more than 60 adults in drift, adult collections represented 14–33% of the total exuvia number, for an average of 24%.

29 April 1974, 225 exuviae. – We left the river the afternoon of 27 April and returned the afternoon of 29 April to find the river bank littered with dead female subimagos which must have emerged that morning. We assume that canoeists had camped overnight and had turned on lights 45 min to 1 hr before sunrise. On 3 May 1974 a similar situation was found at Kennedy

Bridge and the campers were still there: they had turned on lights 50 min before sunrise and enthusiastically described the "big, white flies" they had seen. The only data we can use to estimate exuvia number is that of 1 May 1974 where 47 females flew into two lights (exuvia total 36). The number of females flying into light is dependent on many factors. Further, we do not know the total number of females dead on the bank. We did pick up a random sample of females (98 when counted) which must have represented less than $1/3$ of those present. From this, we give a very rough estimate.

9–11 May 1975. — The river was too high to run drift nets. Presence or absence of emergences were estimated from: 10 adults at light on the 9th; nothing on the 10th; nothing at light on the 11th, but 3 male imagos seen flying over the sand bar.

c) *Experimental*

In order to better understand the response of *Dolania americana* to temperature changes and light, we attempted some experimental work. Experiments in 1973 were run in polystyrene containers (approximately 14 l capacity). These containers were not durable, so we used glass aquaria (23 l capacity) in 1975. For both sets of experiments, mature nymphs were collected from Kennedy Bridge, sand from the bottom of the Blackwater River was used as substrate, the tanks were filled with water from the river, aeration was supplied by air pumps with air stones, and ordinary electrical aquarium heaters maintained minimum temperatures. In 1974 we tried to use flowing water channels with slow current to study *Dolania*, but nymphs drifted out under these conditions as soon as it became dark. The 1973 and 1975 experiments with non-circulating water represent an even less natural condition, but nymphs could not float away. The use of aquaria also meant that the emergence record for any day's hatch would be preserved on top of the water. As will be explained below, *Dolania* cannot fly without the assistance of water current.

1. Temperature. — In 1973, 12 male and 12 female nymphs were kept in an aquarium under natural photoperiod and natural temperatures. After two mornings of low water temperatures (10 °C and 13 °C), we added a heater to prevent water temperatures from dropping below 19 °C; otherwise, water temperatures were allowed to fluctuate naturally. The number of consecutive warm mornings before *Dolania* emerged will be found in Table 6.

There are two problems with the 1973 experiments: 1) we do not know the number of nymphs which died or survived past the end of the experiment, and 2) a few nymphs that had died were replaced with nymphs collected from the Blackwater River on 17 May 1973. While we assume this did not affect results because the river was also cold on 17 May (see Fig. 5), the experiment was repeated.

In 1975, a group of nymphs was held at constant temperatures of $14.5\text{ °C} \pm 2\text{ °C}$ for 6 days before minimum temperatures were raised above 19 °C. As in 1973, maximum daily temperatures and photoperiod were not controlled. Of this group of nymphs, 15 died and 4 survived past the end of the study. Those that emerged are indicated in Table 6 along with the number of consecutive warm mornings ($\geq 19\text{ °C}$) preceding emergence. Included in the 1973 and 1975 totals are a few nymphs that only partially emerged, but they are counted because the thoracic suture of the nymphal skin had opened.

2. Constant temperature and continuous light. — In 1973, we kept one group of nymphs covered over early morning hours and a second group was subjected to various intensities of artificial light switched on $2\frac{1}{2}$ hrs before sunrise (.05 lux to normal indoor illumination). Both aquaria had heaters maintaining minimum temperatures at or above 19 °C and both contained 12 male and 12 female nymphs each which were replenished once during the experiments after some mortality. One male partially emerged in the dark and 17 adults emerged under light. These experiments were of an uncontrolled and preliminary nature.

In 1975 we placed 10 male and 10 female nymphs each in four aquaria with heaters. In an effort to keep water temperatures constant, we adjusted the heaters to match the natural high water temperatures of the day (24–25 °C). While hardly an ideal situation, cooling units were not available. One group of nymphs was kept under natural photoperiod (nLD); one was kept under continuous light (LL, >200 lux) from a 25-watt incandescent bulb with reflector placed 35 cm directly above the aquarium; one was kept in continuous near-darkness (DD, 0.18 lux) with a $7\frac{1}{2}$ -watt incandescent bulb in black receptacle covered by two photographic filters (amber

and yellow) positioned 1.5 m away and out of direct line-of-sight from the aquarium; the last group was exposed to reversed photoperiod (dark from 0700 to 1900 hrs, light switched on from 1900 hrs to 0700 hrs the next day) with identical dark and light conditions already described under DD and LL. The experiments were run only once. The tanks were examined for emergence every 4 hrs \pm 1/2 hr. A normal emergence should occur in the time period between 0300 and 0700 hrs. Besides the lack of replicates, we had problems with temperature and continuous light controls. The nymphs kept under reversed photoperiod all died without emerging, so this experiment should be repeated with a control for low level and gradual light changes as discussed by S. BECK (1968). Results with the other three groups will be discussed with Figure 10.

4. Results and Discussion

a) *Adult habits*

The adult life of *Dolania americana* begins approximately 1 1/2 hrs before sunrise with the emergence of male subimagos. Male nymphs float to the surface of the river and, while floating downstream, the nymphal skin splits along the median line of the thorax and the subimago thorax and head appear. The subimago pulls the wings and the rest of his body through this opening in 8–12 sec, rests 2–3 sec while the wings become rigid, and then flies up from the water — turning initially in an upstream direction.

Table 2 gives times emergence of adults began for the 15 largest documented hatches, expressed as the time the first subimago flew into artificial lights on the river bank each day. On any day, the first male arrived from 0–5 min before the second male, with the number of emerging males then increasing rapidly. The largest number appeared about 1 hr 15 min before sunrise, the last usually an hour before sunrise. Male subimagos later in the morning were very rare (Fig. 3). Nine of the largest emergences began within 10 min of astronomical twilight (Table 2). Males came to light 20 min or more past astronomical twilight on the last six days listed in Table 2, but exuvia and subimago drift samples (Table 3) indicated that emergence actually began much earlier on four of these days. (We lack drift data for 12–13 May 1973.) From Tables 2 and 3 it is obvious that emergence time is not determined by such factors as a clear sky or a bright moon, nor do overcast skies appear to delay emergence.

After emerging, male subimagos patrol the river 1–2 m above the water surface in a slow horizontal flight upstream and downstream over the river. It was difficult to estimate the distance subimagos flew in any one direction — roughly 100 m. They appeared to reverse direction whenever they encountered an obstacle, such as a tree, river bank, or bridge. With many bends in the river at the study site, this occurred frequently.

About 12–15 min after emergence, male subimagos molt to imagos. Those which molted on the ground in front of our lights required 55–90 sec to complete the molt. The subimaginal skin split along the median line of the thorax and the imaginal thorax and head pushed through the slit. The wings were pulled back over the abdomen. Then, pulsating heavily, imagos pulled their wings, abdomen, and caudal filaments out from the subimaginal exuvia. During the molt the prothoracic legs were held horizontally in front of the body while the mesothoracic and metathoracic legs were used for support or grasping; in a few cases, subimagos molted while hanging from the sides of our lights.

Under natural conditions, *Dolania* never molts on the ground and we know that *Dolania* subimagos avoid such objects as trees so we assume *D. americana* does not molt there. We have watched male subimagos molt to imagos while floating down-

Table 2. Beginning emergence times for 15 large emergences of *Dolania americana*, expressed as the time the first male or female flew to artificial lights near the river

Date	Relative Size of Hatch ¹	Sunrise	Hours, Minutes before Sunrise		Nautical Twilight	Weather and Moonlight
			First ♂	First ♀		
30-IV-75	++	0605	1:38	1:01	0:56	moon often obscured by heavy, moving clouds
30-IV-74	++	0605	1:35	0:53	0:56	fog; no moon
2- V-74	+	0603	1:32	0:48	0:56	light clouds, haze; no moon
3- V-75	+++	0602	1:31	0:38	0:57	heavy clouds covering moon, occasional rain
20- V-73	++	0550	1:30	0:50	0:59	moon often obscured by moving clouds
1- V-75	+++	0604	1:29	0:49	0:56	moonlight visible through thin cloud cover
23-IV-74	++	0612	1:27	ND ²	0:55	scattered clouds; no moon
28-IV-75	++	0607	1:25	0:56	0:56	clear, mist above treetops, moon visible
1- V-74	+	0604	1:25	0:49	0:56	clear, light fog; no moon
21- V-73	++	0549	1:10	0:51	0:59	fog, moon visible through haze
13- V-73	++	0554	1:09	0:44	0:58	clear, mist above treetops; no moon
19- V-73	++	0551	1:07	0:40	0:59	scattered clouds covering moon
24-IV-74	+	0611	1:06	0:46	0:55	clear; no moon ³
14- V-73	+	0553	1:01	0:36	0:58	clear; no moon
12- V-73	+	0555	0:55	0:45	0:58	clear; no moon
Averages			1:20	1:29 ^{1/2}	0:47 ^{1/2}	0:57

¹ Estimates from exuvia count in drift nets at sunrise (-2 hr to +15 min): +++ large, 501-3000; ++ moderate, 101-500; + small to moderate, 36-100.

² ND=no data.

³ Unusually cold morning discussed in text.

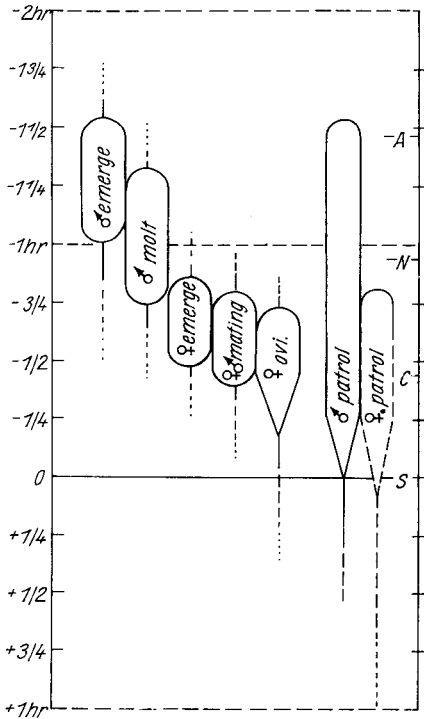


Fig. 3. Schematic diagram of a representative day's emergence of *Dolania americana*. Normal times of activity are enclosed within ovals; unusual ranges are indicated by lines, and extreme records by dots. Note that females patrol only until eggs are fertilized, so extreme records for patrolling females indicate absence or scarcity of males. Abbreviations: *ovi.* = oviposition; *S* = sunrise; *C* = civil twilight; *N* = nautical twilight; *A* = astronomical twilight (general data from 2-V-74).

Table 3. Exuviae and male subimagos of *Dolania americana* collected in surface drift 1–2 hrs before sunrise. “% of Total . . .” refers to the % contribution of the first hour's exuvia drift sample to the total collected over 2 1/4 hrs

Date	Hours before Sunrise			% of Total Exuvia Drift ¹
	2–1 1/2	1 1/2–1 1/4	1 1/4–1	
14- V-73	1	0	3	9.8
19- V-73	0	1	3	2.5 ²
20- V-73	1	0	6	2.8 ¹
21- V-73	2	0	11	4.5
23-IV-74	ND ³	9	14	19.6 ¹
24-IV-74	ND ³	7	6	20.7 ^{1,2}
30-IV-74	0	0	11	8.5
1- V-74	0	0	5	13.9 ²
2- V-74	1	1	5	13.0 ²
28-IV-75	2	18	60	17.6
30-IV-75	3	15	313	21.4 ¹
1- V-75	3	6	154	5.6 ¹
3- V-75	1	2	26	3.9
6- V-75	? ⁴	? ⁴	6 ⁴	0.9

¹ Occasional male subimagos are included in the other columns because they can be the first indicators of a day's emergence, but they are excluded here; if used, the error introduced would increase percentages from 0.5–1.7%.

² Small hatches (35–60 exuviae).

³ ND=no data.

⁴ Only one sample was taken covering entire hour.

stream on the surface of the river and we do find partially molted subimagos in drift samples, indicating that *Dolania* molts on the water. We have never seen male subimagos molt in the air, but we do not wish to totally discount this possibility. An argument exists in the literature (reviewed by EDMUNDS, 1956, BRITT, 1962) concerning a similar molt by *Ephoron album* (SAY). *E. album* has been observed to molt on trees, bushes, or on the water, but BURKS (1953) believes *Ephoron* can molt in the air.

On the morning of 24 April 1974 a sudden cold wave dropped air temperatures from 10.5 °C to 7.5 °C over the two hours preceding sunrise. Water temperature did not drop below 19 °C until after the *Dolania* hatch, but air temperature was 9 °C at the time of the male subimaginal molt. Males did not live until females emerged, and many males were seen floating partially molted on the water surface.

Wind can also adversely affect the hatch. On one windy morning (29 April 1972), males and females appeared and were quickly blown away by the wind. While sudden cold and windy conditions are rare, rainy mornings are quite common. Rain, as on 4 May 1975, does not seem to have any effect on the hatch, although we have never seen a heavy morning rain.

In general, males complete the molt to imagos before females appear. Female subimagos began to emerge approximately 47 min before sunrise (Table 2). Table 2 also gives the times of nautical twilight, although females usually appeared some minutes after this standard reference. Total observed range is given in Figure 3. The manner of emergence is the same as that described for males. Female subimagos never molt to imagos; they remain subimagos through mating and oviposition until death. By retaining the subimaginal skin, the slow-flying females avoid the hazards of a final molt. Also, the subimaginal skin on the female wings appears to increase the wings' reflective quality and thus their visibility to males.

Dolania adults cannot fly from a stationary surface. Under natural conditions, males and females are given enough lift to get into the air by the speed of the water current and then continue to fly throughout their adult lives. However, all adult stages are photopositive and any type of artificial light placed near the river will attract them. Those adults which landed at lights could not fly unless picked up by hand and thrown into the air. This attraction to light normally lasted until shortly after the male molt and female emergence, or until both sexes were present above the river. Male imagos, in particular, were more attracted by female subimagos than by our lights on the sand bank.

After emerging, female subimagos also begin to patrol. They flew in an almost level, slightly undulating pattern 1–2 m above the river, occasionally rising vertically upwards for a few metres and returning to more level flight. As soon as female subimagos were visible, the male imagos increased their flight speed in pursuit. The compound eyes of the males are large and well developed, and male imagos appeared to have no difficulty recognizing patrolling females. Males seemed to be first attracted by the reflected light from the large, white wings of the females. The female wings were so very apparent in the dawn light that we could identify flying females long before we could distinguish male imagos.

Mating begins soon after female subimagos appear, with heavy mating activity continuing until about 1/2 hr before sunrise. A male imago flies up behind a female subimago, assumes a near-horizontal position under her, bends the tip of his abdomen up, and recurves the genitalia forward over his body in alignment with the female abdomen. Copulation usually required 1–3 sec, although it occasionally lasted up to 6 sec. Then both individuals flew their separate ways. We have often seen several males mate with the same female, and males can mate several times.

The forceps of the male imago are much shorter than the penes and we cannot determine whether or not the forceps are used to grasp the female abdomen. Similarly,

the male fore legs are atrophied and apparently do not grasp the female thorax, but we could never observe these details clearly.

Following mating, the females lay their eggs on the water surface in areas of strong current. Eggs of Behningiidae are the largest mayfly eggs known (KOSS and EDMUNDS, 1974): live *Dolania* eggs measure .53–.60 mm by .75–.82 mm when taken from fresh

Table 4. Egg counts from mature female nymphs of *Dolania americana*. Data for 30-IV-75 include counts from 11 reared female subimagos

Date Collected	Number	Mean	Standard Deviation	Range
26-IV-69	9	120.2	22	84–153
7- V-71	14	100.9	14	70–128
4-VI-71	6	93.2	7	80–102
14–17-V-73	10	62.1	18	37– 96
23-IV-74	10	82.9	41	24–161
3- V-74	10	75.1	20	45–108
30-IV-75	23	96.0	19	37–123
Average		91		

female subimago abdomens. Each female carries an average of 91 eggs (Table 4). The eggs are extruded individually. A female flies above the water surface, touches her abdomen to the water, lays one egg, and then flies upstream a few metres to repeat the process. Then she begins to lay two or three eggs at a time. Later, she lands on the water, floats for a time, oviposits in the same manner, and then flies back upstream. Finally she cannot break the surface tension of the water and drifts downstream, still laying the remaining eggs. Sometimes a male will follow a floating female. If she flies up they mate; if not he turns away after 15–20 sec.

It was possible to follow the oviposition patterns of individual females from the time they mated until they were finally carried out of sight by the river. Then, studying females ovipositing in buckets, we determined that the time needed for one female to lay one egg was approximately 1 sec. From this, we assumed that the number of seconds that any female was in voluntary contact with the water approximated the number of eggs laid. While patterns of oviposition varied somewhat from one individual female to another, the great majority of eggs must have been laid before the female was finally entrapped by the river. This conclusion is supported by a very few eggs collected from a large number of females in the 1975 surface drift samples. Also, since we could watch individuals mate and oviposit in one small section of the river, it seems clear that an upstream flight for oviposition, common in many members of the Ephemeroidea (RUSSEV, 1973; FREMLING in RUSSEV, 1973), does not occur in *Dolania*.

On occasion, male imagos formed swarms over a marker (usually a log) in the river, flying up vertically and dropping straight down in the typical Ephemeroptera behavioral pattern characterized by BRODSKY (1973) as "Type A." When a female flew through the swarm, three or four males left the swarm, chased her, and mated with her. To our knowledge, this is the only mayfly reported to exhibit two types of swarm behavior.

The more usual *Dolania* patrol flights, similar to "Type C" of BRODSKY (1973), continued into the early morning. Male imagos patrol in the same way as male subimagos, except that imagos fly over the water and sand banks while subimagos patrol only over water. Both subimagos and imagos fly upstream and downstream equally.

In flight, the male body is horizontal with the prothoracic legs pointed straight forward; the caudal filaments flow back and are slightly raised and slightly spread. Male patrol flights were timed at 5.0–8.5 km/hr, averaging 6 km/hr. Males fly much faster when pursuing females, but we could never make estimates of their speed.

Female subimagos will continue to patrol if males are absent (cold morning of 24 April 1974, small hatches of 4–6 May 1974). On the cold morning the females flew over the river and sand bank, where we were able to time their flight speed at slightly over 4 km/hr. Many landed on the water, which makes us suspect that they too were affected by the cold, but others kept flying until sunrise. On the warmer mornings of small hatches, isolated females sometimes flew vertically up to 10 m above the river, circled, reversed direction, and flew down again toward the water. Usually they patrolled back and forth at about 2 m, flying up high only occasionally. These females finally flew from our sight without ever attracting a male.

On mornings of normal hatches, when both males and females were present, most activity had ended by civil twilight (approximately 25 min before sunrise). At this time, a majority of females were already floating downriver and males were patrolling alone. Occasionally males encountered a stray female and mated with her; the latest observed mating occurred 5 min before sunrise. Activity continued to decrease until, by sunrise, only a few males were flying and a few females were floating. We have seen males in flight up to $\frac{1}{2}$ hr after sunrise, and the latest record of a patrolling female was 1 hr after sunrise. These are exceptional records (Fig. 3). For all practical purposes, the life of an adult *Dolania* ends by sunrise.

Dead individuals float downstream to quiet areas where they form large masses of mayfly bodies. Various birds, bats, and fish actively prey on this mayfly, and spiders build webs between branches of dead logs in the river during the *Dolania* hatch.

b) Comparison with *Behningia*

Adult behavior of a behningiid has been reported only once. KEFFERMÜLLER (1963) described a mass swarm of *Behningia lestagei* (?) from the Warta River, near Uniejow, Poddebice District, Poland, 24–25 June 1962.

B. lestagei emerges in June while *Dolania americana* emerges in late April or May. Both species emerge when the weather warms. KEFFERMÜLLER (1963) specifically mentioned that the 1962 *Behningia lestagei* hatch occurred after one week of warm weather, 22–23 June being hot, and the same is basically true for *Dolania* (Figs. 5–8). Essentially, the only differences in seasonal emergence result from different climates at different latitudes.

Hourly emergence times for *B. lestagei* and *D. americana* are also similar. KEFFERMÜLLER (1963) reported seeing *Behningia* adults at 0320 hrs, or 1 hr before sunrise. Both species emerge floating downstream on the river. For *B. lestagei*, greatest swarming activity occurred at 0400 hrs, or 20 min before sunrise, and the swarm was finished by 10 min after sunrise. These times are 15–30 min later in relation to sunrise than the times we report for *Dolania*. At latitude 52° N in June, there is no astronomical twilight, nautical twilight occurs at 2 hr 7 min and civil twilight at 49 min before sunrise; however, both species definitely complete their adult lives within a few minutes of sunrise.

Morphological descriptions of adults are given by KEFFERMÜLLER (1959) for *B. lestagei* and EDMUNDS (in press) for *D. americana*, but we reemphasize here the conspicuous white wings common to the female subimagos of both species. Females remain subimagos in *Behningia* and *Dolania*, and female behavior is similar in many ways. Females can land and fly off the water, but they cannot fly up from the ground. KEFFERMÜLLER (1963) attributed the inability to fly to the fact that the body was

strongly recurved, forcing the insects onto their backs. The same phenomenon occurs in *Dolania*, but more in the males than in the females; still, even those insects which do remain right-side-up cannot fly unless given a little extra lift.

KEFFERMÜLLER (1963) did not observe mating in *B. lestagei*. She did describe the approach of males to females, which seems identical with that we have observed in *Dolania*.

Differences between the genera are most noticeable in flight behavior. Male imagos of *B. lestagei* and *D. americana* fly straight and reverse direction when they encounter obstacles, but there the similarities end. KEFFERMÜLLER (1963) reported that males of *B. lestagei* flew so fast that they resembled ricocheting rubber balls, that they flew close to the water surface often touching the water with their caudal filaments, that they could land repeatedly on the water and fly again, and that the flutter of their wings was audible. The flight of *D. americana* is comparatively slow and quiet, and *Dolania* males avoid the water and cannot fly again if the imago wings should touch the water. The patrol flight speed of 6 km/hr for *Dolania* is about normal for Ephemeroptera generally (GRANDI, 1973), including even those species which display the typical "Type A" (BRODSKY, 1973) or "pendular" (GRANDI, 1973) swarming behavior. However, the flight speed of *Dolania* can increase when males are pursuing females. *Behningia* has a wing venation (EDMUNDS and TRAVER, 1959) and a thoracic musculature (BRODSKY, 1974) adapted for swift speed flight similar to those adaptations in the Oligoneuriinae, which would account for the observed differences between the two genera of Behningiidae. Recent authors (EDMUNDS and TRAVER, 1959; GRANDI, 1973; BRODSKY, 1973) stress that these morphological adaptations for speed flight have evolved independently in different phylogenetic lines of Ephemeroptera.

c) Polymorphism

Soon after we began studying the adults of *Dolania americana* in the Blackwater River, it became apparent that the adults were polymorphic. Many collections contained female subimagos with a predominately white body and female subimagos with a strikingly dark blackish-brown body.

The dark female morph has a uniformly dark brown head. The thorax is dark brown with the mesonotum dark blackish-brown. The darker colored leg marks of

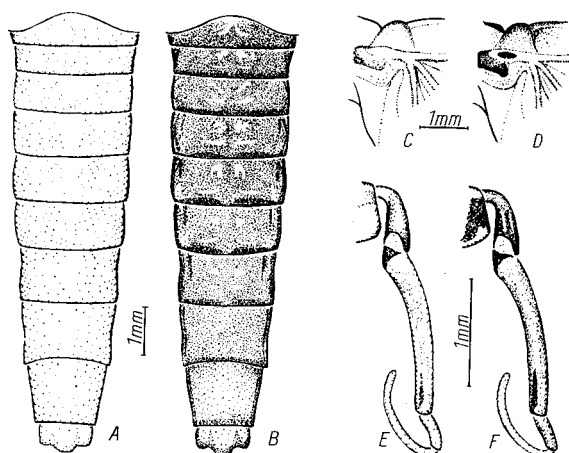


Fig. 4. Comparison of light (A, C, E) and dark (B, D, F) female subimago morphs of *Dolania americana*: A, B dorsal view of abdomen; C, D base of fore wing; E, F fore leg.

the light female morph are extremely dark in the dark female morph (Fig. 4 F). The abdomen is dark brown except for darker and paler marks as in Figure 4 B. The wings of both morphs are white, but the basal sclerotized portions are darker in the dark females (Fig. 4 D). No size differences occur between the two morphs. Occasionally a dark female morph has a lighter colored abdomen, but such individuals are rare.

No dark male morph has ever been found. Occasionally a male imago will have a little darker thoracic and abdominal marks, but only a few have been collected and they are not easily distinguished from other male imagos.

We have studied adults from the Shoal River, Florida, and Upper Three Runs Creek, South Carolina, without finding any dark morphs; however, these collections were small and further study will be necessary. To learn if there were seasonal or hourly differences in emergence times between the two morphs, we ran regular drift samples during the *Dolania* hatch but found no temporal differences in the pattern of activity — as an example see Table 1. Visual observations could not detect differences in general behavior, patrolling, mating, or egg laying. In fact a single male imago has been seen mating with first a light and then a dark morph, and vice versa.

Table 5 gives the percentage of dark female subimaginal morphs in the collections for 1973–1975. Although we have lost the general collections for 1973, we can remember

Table 5. Percentage of dark female subimago morphs of *Dolania americana* collected by different methods, 1973–1975. Range of daily percentages is also indicated in Part A

		No. ♀	% Dark ♀ Morphs	Sex Ratio (No. ♂: 1 ♀)
A. Drift Collections ¹	1973	134	1.5 (0–4.3)	.67
	1974	82	4.8 (0–10)	.67
	1975	1251	2.6 (0–5.5)	.66
B. General Collections ¹	1973	ND ²	ND ²	ND ²
	1974	418	32.3	1.92
	1975	125	16.8	3.32
C. Light Traps (1-V-74) ¹	white	24	37.5	1.42
	UV	23	52.2	1.52

¹ Details of drift nets, sweep nets, lights, and other methods in methods.

² ND=no data.

the number of dark morphs as being extremely small. The ratio of males to females in Table 5 is only included as an example of how behavioral differences and collecting methods can affect results, the sex ratio being approximately 1:1. While the sex ratio can be estimated from nymphal collections, we cannot estimate percentage of dark morphs from nymphs because all nymphs look identical until shortly before emergence when the imaginal cuticle begins to show through the nymphal exuvia.

Table 5 C shows slight differences in the attraction to light of the two morphs. Unfortunately, there was a small overlap in wavelengths emitted by the two lights, numbers were small, and the experiment was only run once; however, these data suggest one area for future, more carefully controlled research.

Drift samples were collected by a standardized procedure while the general collections represent an accumulation of non-standardized and somewhat subjective methods. Still, the differences between the percentages of dark morphs in drift or general collections (Table 5 A, B) seem to indicate something more than human subjectivity. Perhaps the difference is behavioral (light response, attraction to sand bars,

avoidance of drift nets, etc.), perhaps physical (rate of sinking from surface drift, conspicuousness to predators, etc.). Without speculating further on this aspect of polymorphism, one thing is clear from Table 5: the proportion of dark morphs in the population changed each year. It was largest in 1974, half as large in 1975 as in 1974, and relatively small in 1973.

The annual changes in populations of the dark morphs would seem to indicate that some selection pressure affects the persistence of polymorphism. As there appear to be no clear behavioral or ecological differences between the two female morphs, then selection pressures might affect some other stage of the life history. The dark morphs may be marker morphs carried over from the egg or nymphal stages. BRADSHAW (1973) studied polymorphism in *Chaoborus americanus* (JOHANSEN) and found that large dark yellow morphs represented larvae which broke diapause and pupated rapidly in the presence of long days with food while pale morphs of *C. americanus* were more conservative in their development. Selection favored the dark morph in years with a continuous warm spring and the pale morph in years where the initial spring thaw was followed by refreezing (BRADSHAW, 1973). Because of the many differences between *Chaoborus* and *Dolania*, we only cite BRADSHAW (1973) here to emphasize two points: 1) pigmentation does not cause development but it may be a marker indicating different physiological or developmental patterns; 2) environmental selection pressures favoring a particular morph may occur at a different stage in the life cycle.

Recognizing the possibility that the morphs are markers, we now look at general conditions during the life of each generation of *Dolania* studied (Fig. 2). For that emerging in 1974, the weather in Northwestern Florida was relatively "pleasant"; there was a warm winter (particularly January 1974) without drought or prolonged flooding. The 1973 emergent generation suffered through record drought (fall 1972) and heavy spring floods. Conditions from summer 1974 to spring 1975 were somewhat intermediate, with heavy flooding in April. We are tempted to believe that adversity favors the light morph and that the population of the dark morph increases in more "pleasant" years. Even if true, we still do not know if high water, low water, temperature, or another unknown factor is truly causative, and much more data is needed before any conclusions can be suggested.

d) Seasonal emergence

The adult emergence of *Dolania americana* is seasonally restricted and generally occurs over a 2–3 week period in late April or May (Figs. 5–7), although we have records of emergence into June in 1971. In 1973, there were 2 exuviae in the surface drift on 26 April, 1 on 3 May, 10 on 8 May, 11 on 9 May, and 75 on 12 May — the day which, for all practical purposes, emergence began (Fig. 5). In 1974 we collected 3 exuviae on 21 April, 16 on 22 April, and 107 on the 23rd; then cold on the 24th suppressed the hatch (Fig. 6). There is little doubt but that we missed the first indications and probably the first emergence in 1975 (Fig. 7). The 1973 emergence began later than those in 1974 and 1975, delayed by a cold, very wet spring season.

The obvious seasonal factors influencing emergence are river depth and temperature. When the weather becomes hot and the river level drops, *Dolania* emerges (Fig. 8). The influence of temperature on seasonal patterns has been recognized from at least the time of IDE (1935) to present studies (THIBAUT, 1971; LANGFORD, 1975). IDE (1935) reported that higher temperatures shortened the emergence period of the species he studied, as also seems to be the case in *Dolania*; however, this was not true for many of the species discussed by LANGFORD (1975). The relationship of high water level to emergence was also noted by LANGFORD (1975). For *Dolania*, this relationship

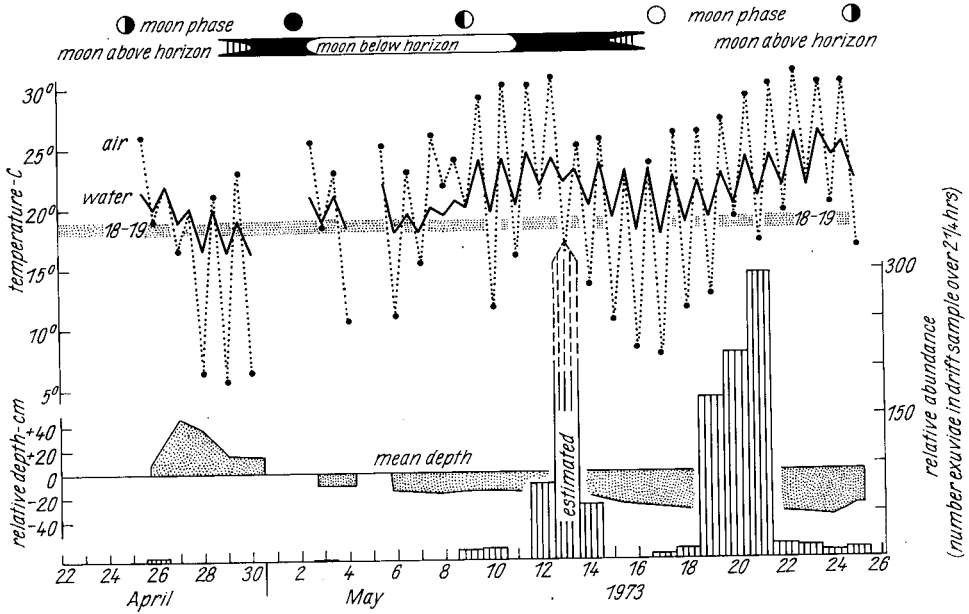


Fig. 5. Seasonal emergence of *Dolania americana* in 1973. Low air and water temperatures, moon position in relation to horizon, and water level are given for the time of day preceding sunrise when *D. americana* could emerge. Breaks in data represent days when records were not taken.

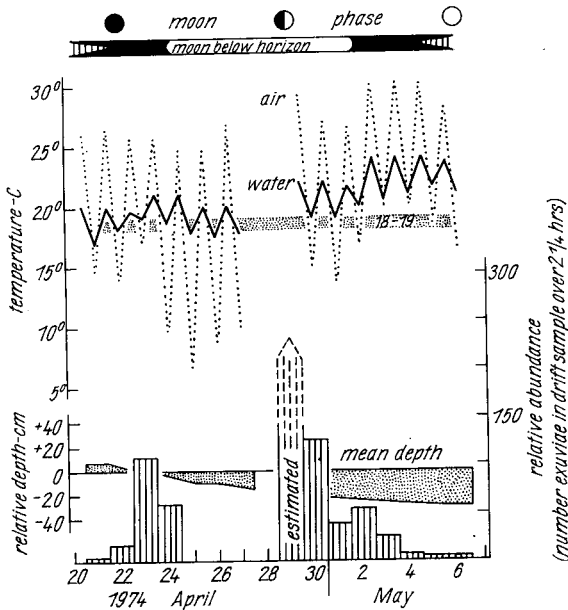


Fig. 6. Seasonal emergence of *Dolania americana* in 1974. Explanation as in Fig. 5.

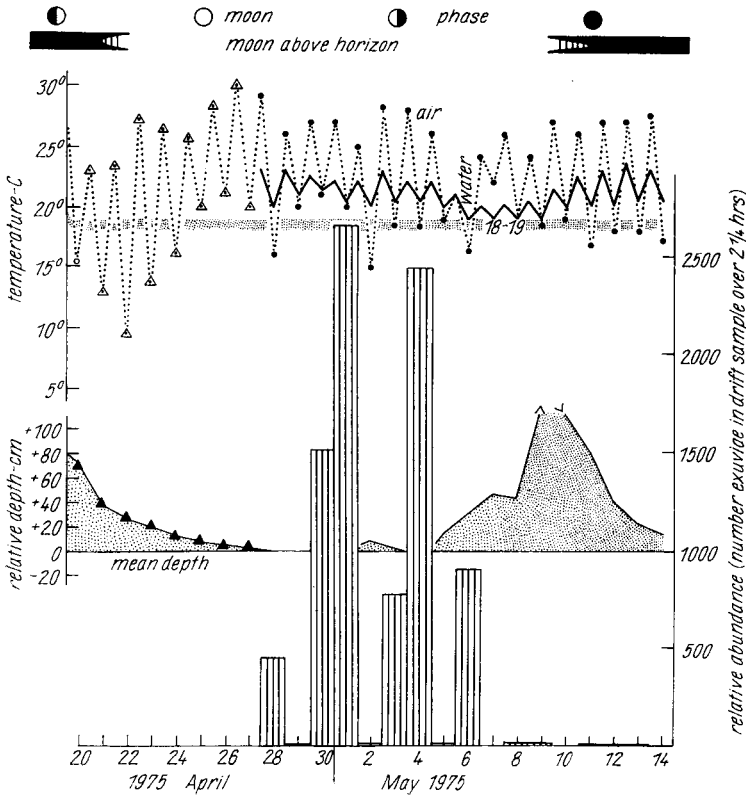


Fig. 7. Seasonal emergence of *Dolania americana* in 1975. Explanation as in Fig. 5, except for supplemental data: open triangles = minimum and maximum air temperatures recorded at Coldwater Tower (DOF); dark triangles = daily mean water level at Highway 4 (USGS).

may be temperature related: when the river is high it has been raining and, when raining, air temperatures are somewhat cooler than the $>25^{\circ}\text{C}$ days which precede the emergence of *Dolania* (Fig. 8). However, there are other explanations (LANGFORD, 1975) which will be discussed later.

The emergences of 1973 and 1974 occurred in waves that were clearly synchronized by changes in water temperatures (Figs. 5–6). In 1975, temperatures remained warm through the emergence period and that emergence became sporadic in character (Fig. 7). An initial temperature-synchronized emergence followed by sporadic emergences is also the pattern reported by FREMLING (1973b) for *Hexagenia bilineata* (SAY). In 1973, there were still a few nymphs in the river at the end of the study, while 2 hrs of fruitless collecting on 13 May 1975 indicated the 1975 emergence had totally ended. Based on after-the-fact analysis of temperature data from Coldwater Tower (DOF), the 1975 emergence could have begun by 25 April; it essentially ended on 6 May. For 1973, we do not know if the remaining nymphs continued to emerge in small numbers or if some other factor acted to synchronize a later mass emergence. (June is never cold in Florida.) Their number was small, so the 1973 emergence might have almost ended. This supposition would require a smaller population in 1973 (apparently true) and would explain why there was no sporadic series of mass hatches following the initial temperature-synchronized emergences. Still, it is also possible that the

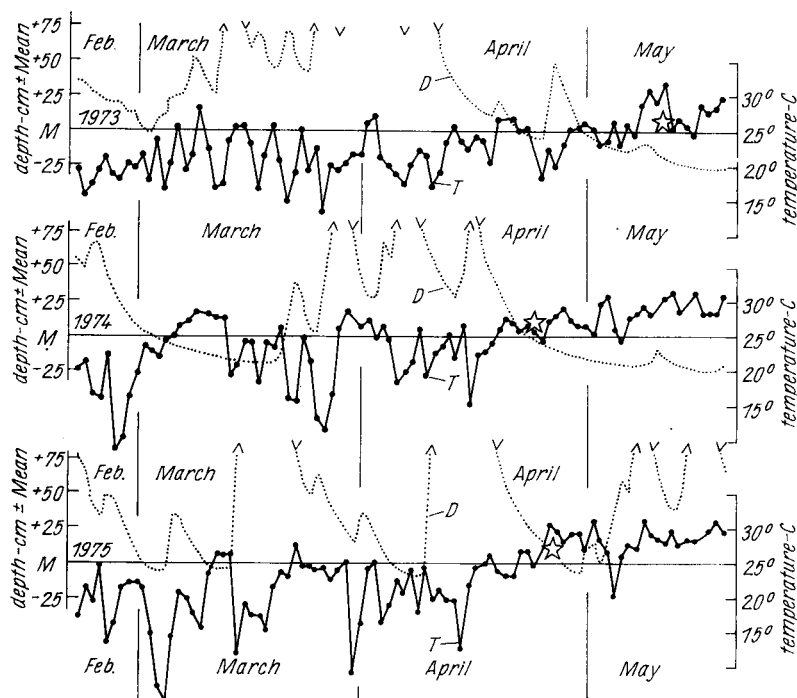


Fig. 8. Daily records of depth and air temperatures from 20 February to 20 May, 1973–1975. Mean daily depth (D) expressed in cm above or below mean depth at Highway 4 (USGS); daily temperature (T) taken at 1300 hrs at Coldwater Tower (DOF). Stars indicate the beginning of emergence each year, although the 1975 emergence is indicated as beginning a few days before observed for reasons discussed in text.

mayfly responds to different climatic conditions in different years with different developmental patterns or behavior.

There is one more characteristic of seasonal emergence which is best illustrated by surface drift patterns for 1975, that of the upstream shift of emergence intensity over the emergence season. We had noted in other years that emergence seemed to occur some days later at Kennedy Bridge than at the field station, and water temperatures are slightly cooler there. The 1975 pattern, uninterrupted by breaks in temperature thresholds, confirms this by the shift in the time the bulk of exuviae and adults were captured in surface drift nets (Fig. 9).

We know that emergence times for *Dolania* are fairly constant (Tables 2–3, Fig. 3). If emergence occurred just at or below the drift net, we should see activity and still catch little to nothing in the nets; this apparently happened on 22 April 1974 when there was more observable activity than indicated by an exuvia count of 16. If emergence began just above the nets, then we should catch exuviae immediately after those known emergence times (as in Table 1). As the emergence moved upstream, the exuviae would arrive later and later. This can be seen in Figure 9, where the middle half (25–75%) of each day's exuvia drift is indicated by diamonds to the left of the adult pattern.

The same pattern can be represented in another way. Because of known emergence times and current speeds, the exuviae collected over the first hour of sampling must represent male subimagos emerging over a short distance upstream. The percentage contribution of the first hour's sample to the total exuvia sample declines over the

emergence season (Table 3). There is one advantage in using these figures (Table 3) to illustrate the upstream shift of emergence: it is possible to include mornings when total drift numbers were small but there was observable flight activity.

The other indicator of upstream shift appears in the female surface drift samples for 1975 (Fig. 9). While males continue to fly after mating and appear sporadically

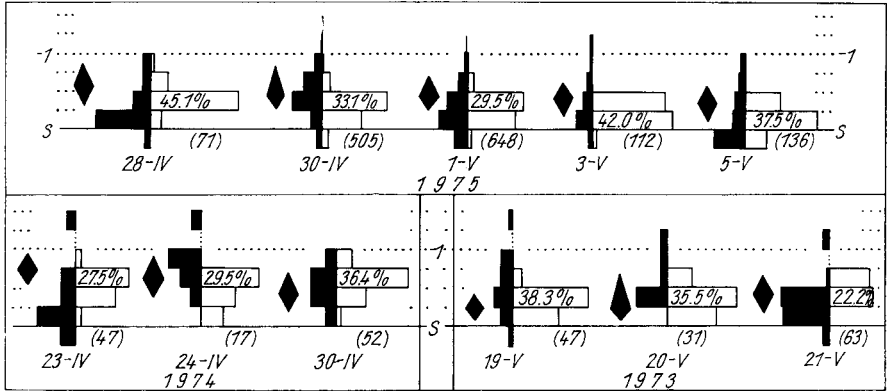


Fig. 9. Percentage representation of males and females of *Dolania americana* in surface drift on days of mass hatch. Black bars = ♂; white bars = ♀; scale indicated on ♀ (a square unit = 10%); total number in parentheses. Diamonds to the left of each figure indicate the time period in which 25–75% of exuviae were collected. Abbreviations: S = sunrise; -1 = 1 hr before sunrise. The date for the last histogram in 1975 is 6-V (not 5-V).

in the drift, females emerge, mate, and begin to oviposit in a fairly rapid time sequence (Fig. 3) so they should appear in abundance in drift samples representing the time period from $3/4$ to $1/4$ hr before sunrise. (Occasional females collected earlier were probably emerging.) When most females arrive in later drift samples, we assume they came from farther upstream.

The drift patterns (Fig. 9) are one more indication that we missed the beginning of the 1975 emergence. The data for 23 April 1974 in Figure 9 would best seem to indicate the pattern for an early season emergence. In spite of low numbers, the drift pattern for 24 April 1974 is included (Fig. 9) to show the rapid elimination of males on that morning of unusually cold air temperatures.

When the emergence season of *Dolania* has been interrupted by cold weather as in 1973, the upstream shift in emergence activity is either not apparent or does not occur. The pattern for 19–21 May 1973 (Fig. 9) even seems to show a downstream shift. Apparently the generalized upstream shift did occur in 1973 (Table 3), but water temperatures warmed a little faster upstream after the short period of cold, thereby disrupting the pattern (Fig. 9). One large tributary, Penny Creek, enters the Blackwater River a short distance above the study area and flows from the east draining agricultural land; the Blackwater River flows down from the north-northeast through forest. Water temperatures are generally about 1 °C cooler upstream on the Blackwater River but, because the river is also shallower upstream, temperatures might respond more quickly to air temperature fluctuations. Penny Creek is .5–1 °C warmer than the Blackwater River, as are certain other tributaries. All tributaries drain slightly different areas and all are shallower than the main river, so that their influence on the temperature of the Blackwater River could theoretically vary with sudden changes in air temperature.

The upstream shift in emergence intensity will not account for the sporadicity of the 1975 emergence (Fig. 7). While heaviest emergence activity must have occurred

upstream from the study site on 3 and 6 May (Table 3, Fig. 9), there was still emergence and visible adult activity at the study area on these days. This is also true for 4 May, although only irregular drift samples and observations were taken because of the rain. There was no observable activity at the study site on 29 April, 2 and 5 May 1975, and any upstream emergence must have been quite small, a conclusion based on exuvia counts of 22, 11, and 16 respectively. Further, many exuviae collected on these dates were not fresh.

We emphasize that data were taken the same way every day in 1975, and that the absence of adult activity and the few exuviae in drift indicate an absence of significant emergence on 29 April, 2 and 5 May. The sporadic character of *Dolania* emergence is not an artifact of the method, a criticism sometimes applied to other records of sporadicity (P. CORBET, 1964). In discussing advantages of synchronized emergence, P. CORBET (1964) cited the opportunity for mating as particularly important in insects with short-lived adults. Synchronization becomes even more essential in *Dolania*, for there is no indication of parthenogenesis (unpublished data). Still, we do not know how emergence was so precisely synchronized in 1975.

Figures 5–7 also seem to indicate rather striking changes in the population of *D. americana* from one year to the next. Realizing that drift totals and drift patterns are influenced by the length of a section of river in which emergence occurs, the length of the emergence season, the speed of the current, and possible population fluctuations in nearby tributaries, we hesitate to interpret or estimate numerical values for these changes. Total populations may also be affected by annual changes in fecundity of females (Table 4), but these surprising results are possibly an artifact of the method as small and random samples of mature female nymphs and a few reared subimagos were dissected for egg counts. At this time, we only wish to indicate that apparent population fluctuations occur.

e) Factors initiating emergence

From observations on behavior it appears that our exuvia count must drop below 16–25 (depending on general factors already discussed) before the emergence is so small that normal behavior patterns are changed and females must engage in a long patrol flight. Such small emergences only represented 1% of the total emergence in 1975 and 5% in 1973 and 1974. Most emergence occurred in mass. Recent authors who have studied emergence (P. CORBET, 1964, HUMPESCH, 1971, THIBAUT, 1971, FREMLING, 1973a b, LANGFORD, 1975) suggest the following factors as possibly important in influencing or synchronizing emergence: temperature of air and water, light, moon phase, flow, humidity, wind, rainfall, photoperiod, successive instars, hormones, and internal rhythms.

Several of these can be eliminated rather quickly. The possibility that the sporadic emergence of *Dolania americana* in 1975 represented rapidly maturing last instars whose growth was temporarily suppressed by hormones cannot be seriously considered because of the short 2-day time period between sporadic hatches; penultimate instars mature over a longer time. Also, aside from their influence on conditions in the water, we can disregard all those factors in the air — air temperature, humidity, rainfall, wind. The emergence of *Dolania* is apparently similar to that of *Ephoron album* studied by BRITT (1962) in that the emergent mayfly cannot retreat after it reaches the river surface. Drifting nymphs were never collected and nymphs which came to the surface to emerge did so in spite of adverse air conditions such as cold or wind which killed them or disrupted normal mating and oviposition. According to FREMLING (1973a b) the same is true for *Hexagenia bilineata*.

We recorded moon conditions throughout the study (Table 2, Figs. 5–7) and saw large emergences in the presence of a bright and completely visible moon only twice

(30 April 1972, 28 April 1975). More often than not, *Dolania* emerged on cloudy or foggy mornings (Table 2) but such weather is quite common during April and early May in Florida. We very much doubt that moon phase, moon visibility, or intensity of moonlight have any direct influence on the emergence of *Dolania*.

Effects of increased daylength on emergence of *D. americana* are unknown. No data have been published for any species of mayfly although daylength is suggested as a possible factor affecting emergence by many authors (recently THIBAUT, 1971, LANGFORD, 1975). The effects of increased daylength on seasonal emergence have been documented for other aquatic insects. LUTZ (1968) indicated that the separate and combined effects of increased temperature, daylength, and degree of nymphal maturity quicken the nymphal development of *Lestes curinus* SAY. In March 1974 a few nymphs of *Dolania* were approaching maturity and theoretically a very few might have been able to emerge (Fig. 8). Whether they did so, or whether they did not because of the shorter daylength, is an open question.

Water temperature is one factor which does have a clear synchronizing influence on emergence. During the study mass emergence did not occur if water temperatures dropped below 19 °C at the time of male subimago emergence, although small emergences began at temperatures above 18 °C. The low temperatures indicated in Figures 5–7 were recorded at the time the first male emerged, or 1–2 hrs before sunrise when there was no emergence. Sometimes temperatures continued to drop. The daily low water temperature had to drop below 18 °C before it could suppress emergence for the following day.

Water temperature thresholds are important and at least partially responsible for emergence, both seasonally and daily, of many mayflies, but these have seldom appeared in the literature. FREMLING (1973a) reported that *Hexagenia limbata* (SERVILLE) could not emerge below 14.5 °C and *H. bilineata* below 18 °C under experimental conditions; FREMLING (1973b) gave a figure of 19 °C for *H. bilineata*. BRITT (1962) noted threshold temperatures of 15–18 °C for *Ephemera simulans* WALKER. The cessation of emergence after a temperature drop was reported by BRITT (1962) for *Ephoron album*, by HUMPECH (1971) below 8 °C for *Baëtis alpinus* (PICTET), and by LANGFORD (1975) below 15 °C for *Heptagenia sulphurea* (MÜLLER) and *Ephemerella ignita* (PODA) although the latter two species began to emerge at temperatures as low as 12 °C (LANGFORD, 1975). MACAN and MAUDSLEY (1966), after studying the temperature regime of an English fishpond for six years, suggested that 10–11 °C was critical for emergence of *Leptophlebia* spp. THOMAS (1969, 1970) studied emergence patterns of several species of mayflies: from Austria, he showed emergence of *Ephemerella ignita* at slightly higher and *Leptophlebia marginata* (L.) at lower temperatures than those just given (THOMAS, 1969); from Sweden, he found *Heptagenia sulphurea* began emerging at temperatures slightly below 12 °C (THOMAS, 1970). There would appear to be some differences among populations of a species. The study of temperature thresholds is further complicated by the role of temperature in nymphal maturation (discussion of day-degrees in BRITT, 1962, MACAN and MAUDSLEY, 1966, THIBAUT, 1971, LANGFORD, 1975). An emergence threshold may have already been exceeded before the nymph is mature enough to emerge to a subimago.

The temperatures of 18–19 °C given by FREMLING (1973a b) for *Hexagenia bilineata* are identical with those for *Dolania*. Temperatures given for the other species mentioned are lower, but also interesting in that some show a greater variety of range. For insects which cannot test the air temperature before emerging, BRADSHAW'S (1973) explanation of temperature response seems valid: as an aquatic insect approaches emergence, it becomes extremely sensitive to a small change in water temperature, because this indicates a larger change in air temperature. The insect will emerge as long as the water is warming, but a temperature drop means colder air temperatures even if the water temperature does not drop below the threshold necessary to initiate emergence. While we would like to extend this theory to account for the sporadic quality of the 1975 emergence where days with no emergence were accompanied by a slight drop in temperature, mass hatches also occurred with slight drops in tem-

perature (Fig. 7). The temperature thresholds for *Dolania* must be very narrow: when water temperature rises above 18 °C, *Dolania* begins to emerge; when temperature drops below 19 °C, emergence stops.

In addition to functioning as an emergence threshold, daily fluctuations in water temperature (Figs. 5–7) may have a part in synchronizing emergence. W. BECK (1973) attributes the moderate temperature fluctuations in the Blackwater River to the temporizing effect of ground water sources of the river.

Emergences appear to be synchronized in the same manner whether the nymphs are subjected to short periods of cold or longer periods of slightly depressed temperatures, as shown in the experimental results (Table 6). The 1973 experimental group

Table 6. Number of consecutive warm (≥ 19 °C) mornings necessary for emergence of subimagos of *Dolania americana* after experimental period of cold (< 19 °C) water temperatures.

No. warm mornings	+1	+2	+3	+4	+5	+6
No. emerged, 1973	0	0	4	1	8	0
No. emerged, 1975	0	0	3	2	7	1

experienced 2 cold mornings (10 °C and 13 °C), while nymphs in 1975 were held at 14.5 ± 2 °C for 6 days before temperatures were raised. In 1975, mayflies which emerged represented 41% of the total, those which died 47%, and those which survived more than 7 days 12%; we lack exact numbers, but percentages in 1973 seemed similar. Both groups emerged after 3–5 mornings of water temperatures ≥ 19 °C, with an apparent peak on the 5th morning (Table 6). Field records are a little more variable, indicating emergence 2–6 days after the end of cold (< 19 °C) water temperatures (Figs. 5–7), but field conditions are also more variable. Under natural conditions, the apparent peak on the 5th or 6th morning would mean a period of nearly a week's warm weather, and most probably warm air temperatures upon emergence.

The experimental data (Table 6) fit the field data quite nicely in 1973 (Fig. 5) and should explain the beginning of emergence in 1975 (Fig. 7). A 5–6 day peak is not evident in 1974 (Fig. 6). Either the time between temperature cues and emergence was shortened, or nymphs cued on a lower temperature, or another factor was present. 1974 was also the year with the warm winter and the large population of dark female morphs.

From Figures 5–7, *Dolania* did not emerge when water depth was more than 35–40 cm above mean depth, and at this depth only once at the end of the 1975 hatch. Usually, the level of the river was close to or below mean depth. This may be, in part, a seasonal factor associated with general temperature conditions. However, in 1971 emergence stopped for one day after a heavy rain and higher water and resumed the following day. While this might have been a sporadic emergence as in 1975 with no hatch that day in any case, this suppressive effect of high water was also found for mayflies in an English river by LANGFORD (1975). He offered two possible explanations: either mayflies are sensitive to current speed and cease normal activity above an implied current threshold (ELLIOTT in LANGFORD, 1975); or, increased turbidity with its associated depletion of light on the river bottom suppresses emergence (LANGFORD, 1975). While we have no information to prove or disprove the first suggestion the second seems more likely for *Dolania*. We do know that *Dolania* is extremely sensitive to light. It appears that with increased turbidity the necessary wavelength or light intensity cannot penetrate to the river bottom. S. CORBET, SELICK and WILLOUGHBY (1974) showed that *Povilla adusta* NAVAS exhibited a lunar periodicity of emergence in lakes with clear water, but not in lakes with turbid

water. Clarity of water seemed to affect the synchronization of nocturnal emergence activity for *Povilla* (S. CORBET, SELICK and WILLOUGHBY, 1974).

As adult behavior occurred at specific times during the pre-dawn hours, we took readings of light intensity at these times. Normally, male subimagos began to emerge at light intensities of .03 lux and female subimagos at .04–.05 lux. Readings were lower on some foggy mornings, but we tend to discount the lower readings because of difficulties with light meters under fog conditions. The lowest visual readings for mating were .05 lux, but this appears to be a minimum for human observations rather than *Dolania* activity; we could see female subimagos ovipositing before it became clear enough to clearly observe mating. Oviposition began after female subimagos had mated, and our data indicated no correlation between oviposition and light intensity.

We do not know what portion of the spectrum is important for synchronizing adult activity as the meters measured only total visible light. For nymphs of *Baëtis* and *Ephemerella*, CHASTON (1969) found their greatest sensitivity was to light in wavelengths of 500–600 nanometres, indicating that lux was an acceptable unit of measurement in studying drift. Still, the total response of *Baëtis* and *Ephemerella* varied at different wavelengths (CHASTON, 1969). Most *Dolania* activity occurred before sunrise, so ultraviolet and the lower portion of the visible light spectrum (or a combination of both) may be responsible for synchronizing activity. Also, wavelengths must be able to penetrate water to the bottom of the river for we know that nymphs of *D. americana* do not drift or swim about before emergence.

While light is important for adult behavior of mayflies, the literature on the subject is limited. PLESKOT and POMEISL (1952) studied the specific visual light intensities necessary for emergence and mating of *Torleya belgica* LESTAGE (a synonym of *Ephemerella major* KLAPÁLEK). HUMPESCH (1971) noted visual light intensities necessary for emergence of *Baëtis alpinus*, and TJØNNELAND (1960, 1969) discussed the effects of light intensities on the mating activities of several species of mayflies in Uganda.

Years of observation and light readings convince us that light is responsible for emergence times of *Dolania americana*, and at specific levels between 0.3–.05 lux. In discussing methods of studying insect photoperiodism, S. BECK (1968) suggested that light levels of 2–20 lux would be acceptable for studying scotophase (dark), and gave extreme examples of .1 lux for a few species. CHASTON (1969) found that light thresholds below 7.2 lux (laboratory experiments) and 1.5 lux (field data) initiated drift in nymphs of *Baëtis*, *Ephemerella*, and other invertebrates. *Dolania* emergence in the Blackwater River fell well below these levels, but *Dolania* emerged at all light levels used in the 1973 and 1975 experiments. The actual influence of light appears to be this: that *Dolania* is sensitive to the slight changes of light in the morning sky associated with astronomical twilight, and that emergence is photoperiodically entrained by this synchronizer or "Zeitgeber" (terminology in this paragraph from S. BECK, 1968).

On the morning after heavy rain, there was no emergence when the river was high and muddy although we know that sometime during the morning light levels will increase on the river bottom. Any influence of thermoperiod (temperature) would not be precise enough to account for this absence of emergence. This leads us to believe that an endogenous rhythm is involved — i. e., *Dolania* will only respond to a light threshold at one time of day.

There seem to be no conclusive experimental studies on endogenous rhythms in mayfly emergence, although the existence of such a rhythm was strongly suggested by MÜLLER (1973) who correlated the field emergence data of THOMAS (1970) with known light levels in subarctic summer. Also, HARTLAND-ROWE (1958) and P. CORBET (1964) suggested that the lunar emergence of *Povilla adusta* might be under control of an endogenous rhythm positioned in the early larval life by a refined response to photoperiod. To our knowledge the only controlled experimental study on emergence is that of HUMPESCH (1971) who subjected nymphs of *Baëtis alpinus* to either

continuous light (350 lux) or darkness, and constant water temperatures and chemistry. Under natural photoperiod nymphs emerged from late morning to sunset. Nymphs in continuous light emerged in an arrhythmic pattern, while nymphs in continuous dark did not hatch for several days, then hatched or died during emergence. HUMPESCH (1971) did not conclusively demonstrate a circadian rhythm in the emergence pattern of *B. alpinus*; however, *B. alpinus* turned out to be a poor experimental animal in that its natural emergence pattern covered almost 10 hrs per day. The observed arrhythmicity of emergence could also be interpreted in this way: those individuals who normally emerged in the morning began to emerge earlier and those afternoon-emerging individuals began later under experimental controls. The reported arrhythmicity was not total, and began to show a recurrent evening pattern at the end of the study under continuous light.

Dolania americana, with its precisely timed emergence, should offer clearer results than did *Baëtis alpinus* in that interpretation of endogenous rhythms could be made from a short natural emergence pattern. However, there are some disadvantages in using *Dolania*. Its annual life cycle and short emergence season allow only one experimental try per year and its habitat requirements are quite restricted. For these reasons, as well as a lack of good technical controls, the results we present in Figure 10 on emergence under constant temperature and different light conditions are preliminary and inconclusive.

Under almost constant temperature and natural photoperiod, only one female subimago emerged (Fig. 10). This result is most puzzling, because emergence was greater when both temperature and light were kept at constant levels. Assuming that there was nothing wrong with the aquarium, it supports the suggestion that water temperature fluctuations and light intensity fluctuations must operate together to cue emergence of *Dolania*, and that the absence of one can be more confusing than the absence of both. HUMPESCH (1971) found emergence followed a synchronized pattern under natural photoperiod and constant temperature in *Baëtis alpinus*.

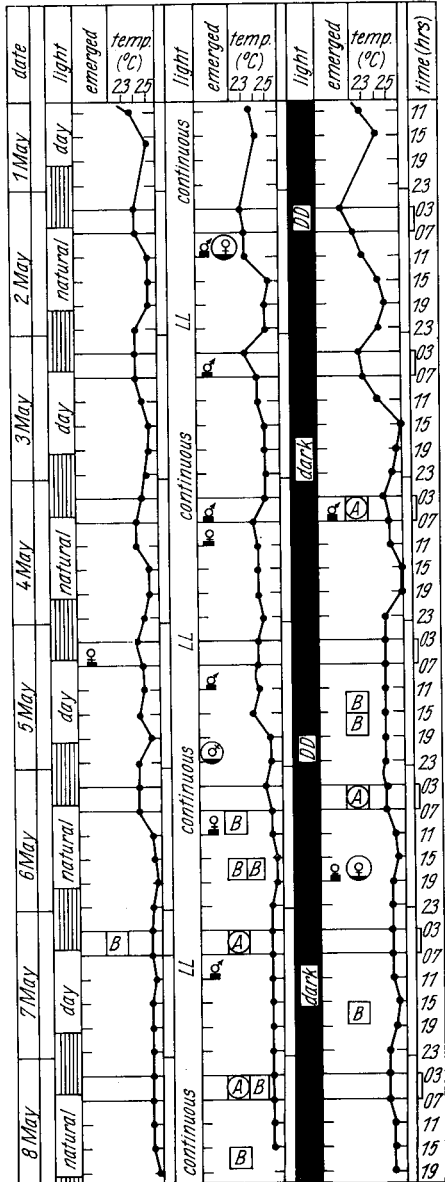


Fig. 10. Emergence of *Dolania americana* under constant temperature and different light conditions, 1975. Experimental aquaria were examined for emergence every 4 hrs. (Normally, emergence occurs between 03 and 07 hrs.) Successful emergences are marked by bar and sex; circled individuals only partially emerged. Squares are discussed in text. The creature that emerged on 5-May between 19 and 23 hrs under continuous light was a male!

The aquarium maintained in continuous light was in a shaded corner away from windows, but it was not sheltered to such a degree that natural daylight might not have had some effect. However, if this light influenced emergence then why didn't natural photoperiod have the same influence on nymphs exposed to it directly? There is an obvious problem here to be studied another year. Emergence did occur with some regularity under continuous light and only one male emerged outside morning hours (Fig. 10).

For nymphs maintained in near-darkness, only three emerged or partially emerged at a visible light level of .018 lux. HUMPESCH (1971) found that some light was necessary for *Baëtis alpinus* to complete emergence; otherwise, subimagos only partially emerged. Emergence can be subdivided into a series of normally continuous processes: the beginning of emergence (rupture of the exuvial thorax), extraction of the subimago from the nymphal exuvia, inflation of wings, flight, etc. Light may be necessary before subimagos will fly off the water since they need a method of orientation, and it may sometimes be necessary in other phases of the emergence process (HUMPESCH, 1971). Light does not seem essential for the beginning of emergence, although the absence of light can delay and suppress emergence to some degree (Fig. 10 and HUMPESCH, 1971).

We arbitrarily counted as successful emergences where the thorax of the nymphal exuvia had ruptured (circles in Fig. 10). Another group of responses marked by squares in Figure 10 are not successful emergences. Squares indicate nymphs who showed many morphological expressions of wanting to emerge but the thoracic suture never opened: swollen abdomen and thorax, a very thin exuvia, caudal filaments and abdomen of the subimago pulled up past segment 9 of the abdomen of the exuvia (Fig. 10, squares "B"). Those squares with a circled "A" (Fig. 10) indicate nymphs apparently so past the point of readiness that the exuvia fell from the dead subimago when it was preserved in alcohol! These and a few other nymphs were found floating dead or near death. Many others died in the sand. Causes of death are unknown, but appear to include a lack of normal water current and high temperatures.

Nymphs of *Dolania* do not feed before emerging. As *Dolania* matures, the gut atrophies to allow space for complete development of reproductive structures and eggs. Mayflies live the last days of their nymphal lives and all their adult lives on stored reserves (NEEDHAM, TRAVER and HSU, 1935). Thus, *Dolania* cannot delay its emergence too long, especially under high temperatures. In the absence of natural synchronizing and phase-setting cues, the mayfly must either try to emerge or die, which perhaps explains those results marked by squares in Figure 10.

We postulate the existence of circadian or endogenous rhythms in *D. americana* from field results and from experimental results just given. More work will be necessary to confirm this theory.

5. Summary

Adult habits and emergence of *Dolania americana* were studied in the Blackwater River, Northwestern Florida, a river of moderate width, slow to moderate current, and shifting sand substrate. Nymphs of *D. americana* burrow into the white, shifting sand. The adult life is crepuscular, beginning about 1½ hrs before sunrise with emergence of male subimagos. Males continue to emerge until about 1 hr before sunrise. Some 12–15 min after emerging, male subimagos molt to imagos. About 45 min before sunrise, female subimagos begin to emerge. Females never molt to imagos, but mate in the subimaginal stage shortly after emerging. Following mating, female subimagos oviposit. A summary of the daily emergence pattern is found in Figure 3 with supportive data in Tables 2 and 3.

Female subimagos and male subimagos and imagos usually fly in a back and forth

horizontal pattern some 1–2 m above the river at slow speed. After mating, female subimagos display a separate oviposition activity. If unmated, females will continue patrol flights until they die, but the flight pattern is marked by periods when the females fly high and circle above the river. Male imagos exhibit two types of flight, the horizontal patrol flight and a vertical swarming flight. While the first type of flight activity occurs more often, the existence of two distinct behavior patterns in one species of Ephemeroptera is most unusual.

The known adult habits of *Behningia lestagei* are compared with *Dolania americana*. The two species of Behningiidae display similar behavior, except for the speed of flight and the altitude above the river at which flight occurs. *B. lestagei* flies faster and lower than *D. americana*, a result, it is assumed, of the more adapted wing venation and thoracic musculature of *B. lestagei*. *B. lestagei* is only reported to exhibit one type of flight behavior.

Polymorphism is displayed by female subimagos of *D. americana*. Although male imagos also show some variation, no distinct morphs can be recognized. The more common female morph is almost white, while the dark morph is nearly black (Fig. 4). Both morphs have white reflective wings, both display the same behavior, and both emerge at the same time daily and seasonally. For these reasons, we suspect that the polymorphism may indicate an environmental selection pressure in another stage of development.

Seasonal emergence patterns are summarized in Figures 5–7, with lowered water level and high temperatures being the factors which initiated the beginning of an emergence season (Fig. 8). The minimum water temperature at 1½ hrs before sunrise (when the day's emergence begins) must be at or above 19 °C for a mass emergence, although a few males and females began to emerge at temperatures between 18 °C and 19 °C. The daily minimum low is 18 °C—when water temperatures fall below this level, emergence is suppressed for some days. Experimentally, *Dolania* emerged after 3–5 mornings of water temperatures at or above 19 °C (Table 6), but field data indicated emergence 2–6 mornings after temperatures rose above 19 °C (Figs. 5–6). When temperatures remained above 19 °C for a long period, the synchronizing effect of temperature seemed to disappear although emergence still occurred in mass at intervals. We have no idea what factor synchronized these subsequent sporadic emergences (Fig. 7).

Exactly how high water suppressed emergence is unclear. High water was associated with lower temperatures on some occasions and there may also be a current threshold above which normal activity is interrupted; however, increased turbidity associated with increased flow and the resulting reduction in light penetrating to the river bottom would seem to be the best explanation in the case of *Dolania*.

Dolania is sensitive to small changes in light intensity, with emergence of male subimagos occurring at visual light levels of approximately .03 lux and emergence of female subimagos at .04–.05 lux. The factor synchronizing the time of emergence on any particular day is apparently the slight change in light intensity occurring with astronomical twilight.

From research just presented, we also show an upstream shift in emergence activity over the emergence season (Fig. 9, Table 3) and a shortened emergence season when temperatures are high (Figs. 5–7). Further study on adults of *Dolania* is required to confirm a suspected sensitivity of the species to shorter wavelengths of light, possible annual changes in fecundity, the probable influence of daily water temperature fluctuations on emergence, and the postulated existence of endogenous emergence rhythms. We also eventually hope to understand the polymorphism displayed by female subimagos and the apparent population fluctuations of *D. americana* in the Blackwater River.

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