The Secret Swarm

In the predawn mass mating of sand-burrowing mayflies, timing is everything

by William L. Peters and Janice G. Peters

Our first reaction to the bizarre sand-dwelling creature was, "Can this be a mayfly nymph?" We were new to Florida, just starting to collect aquatic insects in the state, and unfamiliar with the sand rivers where we would spend much of the next twenty years. After taking a harder look, we detected a similarity to published drawings of the nymph, or immature stage, of the American sand-burrowing mayfly, *Dolania americana*, known then from just a half dozen nymphal specimens in the Western Hemisphere, and not known at all in the adult stage.

Perhaps the unusual nymph had gone largely unnoticed because sand was thought to be an inhospitable habitat. But nymphs hiding in sand could not explain the even more puzzling absence of adult sand-burrowing mayflies. Although we, too, searched, we failed to find living adults. We did, however, find adult remains in spider webs, and for a time we had to be content with robbing webs for dead mayflies, a poor substitute for observing the living animal.

Early one morning a colleague, Jerome Jones, went insect collecting and saw *Dolania* male and female adults mating, and dying, before sunrise. Synchronized, very rapid, mass mating in the dawn hours would explain why adults had never been collected. Our determination to observe a *Dolania* swarm marked the beginning of our research on the maturation and mating of this mayfly. We found that of the two-year *Dolania* life cycle—one year spent as an egg and most of the second year as a nymph—the adult stage accounts for less than two hours or one ten-thousandth of a mayfly's life span, equivalent in human terms to two days in forty-eight years.

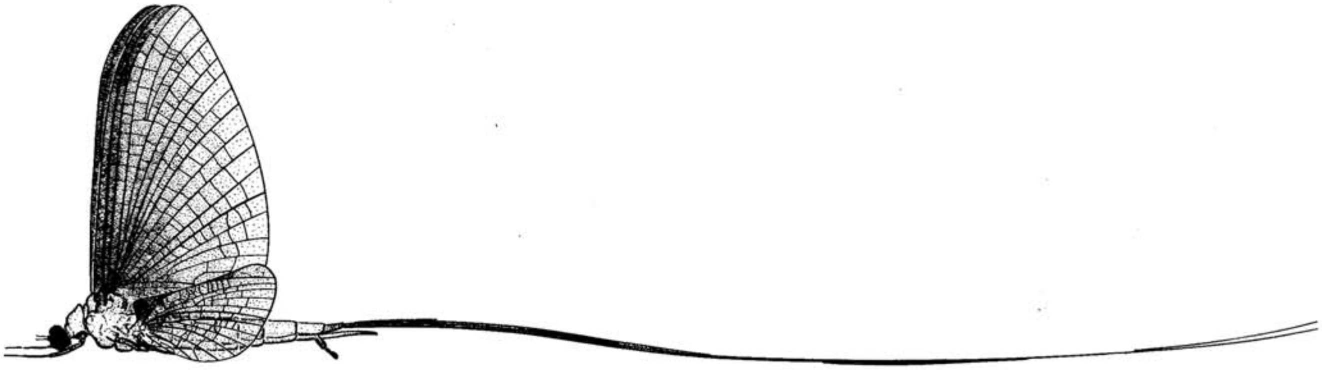
A larval life spent tunneling open-eyed through coarse sand requires some modifications and specializations, and these account for the nymph's unmayflylike appearance. Protective hair patches on large outgrowths on its head give *Dolania* prominent "eyebrows." The middle legs are paddlelike for burrowing, but the front legs are reduced to structures resembling an extra pair of mouthparts, probably to assist this aggressive carnivore in catching sand midge larvae and other prey.

Dolania is not rare, but its distribution is spotty and its habitat is limited. Although its range covers the coastal plain from Louisiana to Virginia, this mayfly's nymphs live only in clean areas of undisturbed, shifting sand bottoms of larger streams and rivers that have never suffered serious ecological disruption.

During our first few years of research, our attempts to observe adults (in the three weeks a year they are likely to hatch) were largely hit and miss. On one beautiful morning we would see nothing; then the next morning a huge swarm would appear. In 1973, we organized friends, family, students, visiting professors, and co-workers for shifts of what turned out to be a thirty-five-day *Dolania* watch. Through the cooperation of Florida's Game and Fresh Water Fish Commission and Division of Forestry, we had the use of a field station and study site on the protected Blackwater River.

A participant in a *Dolania* watch gets up at three in the morning to be on the river with equipment by four. The sun rises around six, but the mayflies may begin to emerge up to one and three-quarter hours earlier. The hatch begins when male nymphs swim to the river surface, shed their nymphal skins, and fly to vegetation or sand banks to complete the next stage of life. Mayflies undergo a preliminary winged stage, the subimago, or subadult, before achieving full, winged maturity. In the case of *Dolania* (and a few other mayflies), the female has dispensed with the final molt and is fully mature as a subimago.

Thus, males have one more life history stage than do females, but to mate, males and females have to be together at the same time and place. To accomplish this meeting, males hatch earlier and rush through the subimago as quickly as air temperatures allow, from twenty-three minutes at 50°F to five minutes at 73°F. Males hasten the process further by breaking off their middle and hind legs and taking to the air as soon as their wings are free of the old skin. Without functional legs, males spend the rest of their lives in flight. They patrol aerially about three feet over the river searching for emerging females. Even an hour before sunrise, females coming out of their old skins are visible to males—and streamside naturalists—because of their large wings, which are a consistently bright, reflective white. Pairs form as soon as the females emerge. Often, males fly above emerging females until the females take wing, then mate



American sand-burrowing mayfly

Janice G. Peters

A male Dolania *subadult undergoing its last molt clings to a tree trunk. When the male completes this molt, it will become airborne for the rest of its life.*
David H. Funk

immediately. If a male is present when a female emerges, she may not spend more than a few minutes in flight in her entire life. The male approaches from behind and underneath the female, copulates for two to five seconds, then disengages and goes on to search for other females. If no males are present, females fly slowly in an undulating pattern, displaying their wings. We presume this display is intended to catch the attention of any available males; at least, the strategy has that result.

We have found no evidence that females choose their mates; females most likely never even see their mates. And while, theoretically, males should favor females with the largest, most eye-catching wings (everything being equal, the large females carry the most eggs), our records show that males chase the nearest available female. When several males pursue a single female, the male that copulates first is the victor. As soon as the mating pair engages, other males turn away. Thus, in competition among *Dolania* males, the race is to the swift. We speculate that by breaking off the "walking legs" during the subimaginal molt, the male not only hurries the completion of that stage but streamlines his body for faster flight as an imago.

A female begins laying eggs almost immediately after copulation, touching the water with her abdomen and dispersing a few large eggs one at a time, then flying to another spot (sometimes mating a second or third time on the way) to repeat the process. In a short time, she tires, falls into the water, and in death is swept away by the current, releasing any eggs left in her body. Even if they are too weak to fly, as long as females are active and flapping their wings, males will follow them. The eggs fall to the bottom of the river and stick tightly to sand grains.

The swarming orgy lasts for about fifteen minutes as more females emerge, mate, begin egg laying, and are carried away downstream. Then, in fishermen's terms, the hatch is over. Fewer and fewer female bodies are seen drifting downstream, while males continue to fly patrol until they too die, usually around sunrise.

Of our thirty-five days in the field in 1973, many mornings were not fit for man or insect: a few mornings brought just a few mayflies; some brought small hatches; and for a couple of mornings the river rose in a swirl of white wings. Over the years, these data have held: at any particular site, about two-thirds of the *Dolania* that emerge will do so in one morning, but usually in two or three, and there will be a few mornings of smaller hatches. Five mornings a year with hatches large enough for quantification—collection and counting of floating skins and dead mayflies—is the norm.

We were amazed that most males and females emerged, mated, laid eggs, and died within the same few minutes of the same day (or two or three dates) each year. Precise timing was critical. We wanted to understand emergence timing, because environmental and man-made effects on hatches or emergence are impossible to assess when we don't know when or how emergence occurs in the first place. With its highly synchronous swarm, *Dolania* became the perfect experimental animal, and the realization that being able to predict emergence would allow us to sleep late some mornings provided extra incentive.

Seasonal temperature and rainfall data enabled us to estimate late April or early May maturation dates. We discovered that an essential factor for emergence is a daily low water temperature of at least 64°F and that this "threshold" temperature must be in effect the day before, rather than the day of, emergence. On mornings with air temperatures somewhat below 50°F, most molting males died trying to achieve the subimaginal molt. Unmated females flew for a while, wings waving, until they also died. Clearly, these mayflies could not predict the weather on the day of emergence; the process was seemingly cued by previous events and, once under way, could not be stopped.

When and how was emergence predetermined? Temperature records showed that emergence correlated perfectly with a strong positive increase in water temperatures the previous morning (compared with two days earlier). Weak water temperature changes over the preceding days gave ambiguous results—sometimes no hatch but often a small hatch—and no mayflies emerged when water temperature fell. Afternoon water temperatures played no role in emergence, but whether the cue for a given day was the temperature at time of emergence or the daily low was unclear, since both occurred between dawn and sunrise at our site on the river.

Events in the life of insects often cue to points in the daily fluctuations of light (photoperiod) or temperature (thermoperiod). For *Dolania*, the temperature cues for emergence and the daily timing of emergence might depend on the coldest time of day or on the dawn light. On one date, the first male, followed by a cluster of other males, usually emerged about one and a half hours before sunrise. On another date, males would begin to hatch out some twenty-five minutes later, when dawn light had visibly increased. Female emergence times also varied but not as dramatically. For the early grouping, males appeared before or at the time of astronomical twilight, the "crack of dawn." We once thought *Dolania* were somehow sensitive to this first streak of light, although we could detect no change in the sky overhead. But the theory seemed increasingly improbable considering that these insects were buried in sand at the bottom of a river and that emergence occurred equally under clear or cloudy skies. Nor could we find any relationship between the water temperature and the time of hatch.

We then postulated the existence of an internal biological clock. To test this idea we experimentally manipulated light, temperature, or both to test effects on emergence and were able to reach some conclusions. When natural temperature cycles were eliminated, *Dolania* nymphs hatched on increasing light, and when light conditions were constant, they hatched at cold temperatures. If temperature and light were both manipulated so that nymphs received no natural indication of daylength, emergence occurred a little later each day. However, experiments were only successful when nymphs had been exposed to the new thermoperiod or photoperiod about a week before emergence. Presumably, timing cues were being set then, because any attempt to manipulate cues in those last few days led to incomplete emergence attempts and death. One factor that directly influenced *Dolania*'s response to experimental water temperature and light fluctuation was the critical 64°F threshold temperature. When light cycles and temperature cycles were experimentally separated (making midafternoon the coldest time of day, for example), nymphs emerged at the time of the coldest temperature when the low water temperature had been below threshold, but they emerged at dawn when low temperatures had remained above threshold. There was an exception: certain nymphs emerged at dawn, no matter under what temperature regime they were reared. These nymphs all came from a different *Dolania* population collected far upstream, where the river was narrow and canopied by trees. There, the daily low temperature came later in the morning and was not associated with dawn light.

Dolania's differing responses can be loosely compared to our experiences with alarm clocks. Critical water temperature acts somewhat like an alarm that rings at the same time each day. Assuming it rings at sunrise, it can reinforce other perceptions of dawn and allow us to anticipate its ring. When the alarm is turned off, an internal rhythm, already established by the alarm, continues for several days, with individual variations. Then, dawn illumination itself becomes a cue. With no alarm and no light, less efficient cues are available, such as the time of coolest temperatures. Finally, in the absence of any cues, another internal biological rhythm is established: in our experiments, *Dolania* emerged a little later each day. Our experimental results helped us understand early emergences in the river following periods of below-threshold water temperatures and later hatches that occurred after five or more warm days with low temperatures above 66°F.

A male frees itself from its old skin. Molted skin sometimes trails behind for a while as males patrol the stream looking for newly emerged females.
David H. Funk

But what happens if low water temperatures have been above threshold but no light has penetrated to the river bottom? Based on experimental results, we assumed that the mayflies would wait until some light eventually penetrated, until they perceived an increase in water temperatures, or until they could wait no longer (internal clocks). In 1985, road construction caused heavy red clay to wash into the river after storms, turning the normally clear waters muddy and blocking the light from reaching more than a few inches into the water. Emergence times shifted to past sunrise, and mating and oviposition occurred in full daylight when the mayflies are especially vulnerable to predators.

Such combinations of field and experimental data contributed to our understanding of how man-made perturbations can hurt insect reproduction in a river. Since aquatic insects depend on temperature and light to set emergence time, such changes as a drawdown of a dam in days prior to emergence might cause abortive emergence attempts and death, while a factor such as heavy siltation might shift the hatch to inappropriate times.

More questions remain. *Dolania* females, but not males, vary in color, with the lightest color forms being the most common and the intermediate forms the rarest. The annual representation of dark forms has varied from 2 percent to 35 percent of the female population. We used a variety of methods to attract and count mayflies and to obtain results that could be analyzed statistically. We know that while dark and light females emerge at the same time, the dark forms, or morphs, are nearly absent from drift nets, are likely to fly farther from the river, and will continue to fly at the site of emergence only if males are absent.

All information is consistent with the hypothesis that the dark females disperse, that is, fly away from their place of emergence, to lay eggs elsewhere. Unlike light morphs, which lay eggs immediately after mating, the dark morphs appear to mate and fly away. From what is known about the behavior of other mayflies, we might expect them to disperse upstream. Sometimes we are rewarded by the sight of the dark morphs floating downstream well after sunrise, but we don't know that these are from the same population. If they are, they have made a one and a half mile round trip. They might also represent another population flying five miles or more from any other direction.

Late arriving dark morphs actively bounce along the water surface with wings raised, in contrast to the light morphs, which flounder shortly after they fall into the water. Still hardy after nearly two hours of adult life, dark morphs long outlive light morphs, which rarely survive more than fifteen minutes unless males are absent. Dark females are not present after every hatch, and large numbers of them are rare. We can only speculate on what is happening. Reproduction is essential, but dispersal is optional and more hazardous where predators abound. We should not expect to see survivors often.

Our Florida data confirm that emergence early in the day furthers mayfly survival by allowing them to mate and lay eggs before most common predators are active. Also, while birds, bats, and dragonflies prey on mayflies on warm mornings, none appear to be very active on cold mornings. Fish, the principal aquatic predators near our study site on the Blackwater River, are not influenced by air temperatures and usually feed whenever *Dolania* swarm. Bernard Sweeney and Robin Vannote of the Stroud Water Research Institute showed that mass hatches served to overwhelm predators (principally beetles in their study stream in South Carolina) with huge numbers of prey; the beetles could not possibly consume enough swarming mayflies to hurt the overall population.

Since the debut of mayflies some 350 to 400 million years ago, their evolution and survival have involved the movement of immature stages into sheltered, specialized aquatic habitats and a reduction in the length of the adult stage. According to George F. Edmunds, Jr., of the University of Utah, and Patrick McCafferty, of Purdue University, the subimago, one of many intermediate stages known from fossil mayflies, has probably persevered as the transitional stage to get insects from the water to the air.

The brief adult life and apparent move toward reproduction in younger stages, called neoteny, is evolving in various ways in all species of mayflies. All adults lack the functional mouthparts that are found in their fossil ancestors, and the adult digestive system has been totally lost. Reproduction by subimagos occurs in females of several families, and while there are no records of mating in nymphs, there is at least one good record of nymphs forming pairs before emergence.

The neotenic trend in mayfly evolution is apparent in *Dolania*, where the less time spent out of the sand, the better. While long-lived dark female morphs may remain in the population as dispersers, evolution favors (at least numerically) the short-lived lighter forms. Even the short, fast, mass swarms and precise timing that bring adults together inevitably sacrifice part of the population to predators. While our immediate research concerns environmental pressures, we can hypothesize that evolutionary pressures also are at work to move *Dolania* from spectacular adult swarms toward reproduction as nymphs in the relative security of the sand.

William L. Peters is a professor of entomology and Janice G. Peters is a research assistant in the Department of Entomology and Structural Pest Control at Florida A&M University in Tallahassee.