PREDATION, CLIMATE, AND EMERGENCE AND MATING OF MAYFLIES

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ABSTRACT

The abbreviated adult life of Ephemeroptera is an adaptation to minimize exposure time to predators. In eight to ten independent specialized lineages adult life is reduced to two hours or less. Predation by Odonata and birds is intensive in the lowland tropics and most unspecialized longer-lived forms emerge as subimagos in the first two hours of darkness, transform to imagos before dawn and mate and oviposit by mid-morning. In temperate regions cool night-time temperatures often preclude the possibility of the tropical pattern; furthermore lessened predation allows other temporal patterns. Temperate mayflies thus have a variety of emergence and swarming times. Short-lived specialized genera are subject to fewer restraints on emergence and swarming times and tropical and temperate forms are similar. Seasonal emergence and coordinated mass emergence are mechanisms for satiating predators. Remote nuptial flight probably evolved as a mechanism of escape from predation; it is assumed that swarm markers are essential to allow remote flight. It is probable that swarm markers are more common in tropical than in temperate mayflies. There is some evidence that ancestral emergence and swarming habits may persist when mayflies disperse to new areas.

Bishop (1973) in his study of the Gombak River of the Malay Peninsula noted that adult aquatic insects were uncommon. Use of a sweep net for sampling adults proved to be almost useless. He attributed the small numbers of adults to heavy predation, especially by numerous insectivorous birds. In two months in Malaysia we did not observe the emergence of a single subimago and we saw very few mayfly imagos in nuptial flight. The abundance and high species diversity in many Malaysian streams suggests that the adults are much more common than these observations indicate. It was obvious that subimaginal and imaginal behaviour patterns in these lowland tropics must be strikingly different from the temperate patterns and apparently different also from tropical highland areas.

About half-way through the Malaysian studies we made a major effort to understand the activity cycles of the mayflies. As the patterns of activity became clear, we compared them with other experiences with tropical and temperate mayflies. The comparisons led us to some interesting contrasts between tropical and temperate forms. It is obvious that some of the factors discussed form a continuum and that the comparison is of extremes of a continuum. This paper contains considerable speculation, but we are hopeful that these broad comparisons will point the way to areas where data is needed.

Apparently many of the activity patterns and adaptations of adult mayflies (subimagos and imagos) have formed in response to selection pressure from predators. Mayfly subimagos are slow and clumsy fliers and are highly vulnerable to predation. Flying imagos are much less vulnerable but resting subimagos or imagos, being Paleoptera, are unable to fold the wings and hide in leaf litter, crevices or other protected areas. The brevity of their winged lives is itself an adaptation to reduce exposure to predation. We agree with Bishop (1973) that birds are serious daytime predators in Malaysia. We believe, however, that the most significant day-time predators are Odonata, and birds are secondary. Many mayflies are killed also in spider webs, but the webs are probably equally effective, day or night. The only significant night-time predators are bats. Both Odonata and bats are generally more abundant and diverse in the tropics. It is abundantly clear that predation on mayfly subimagos and imagos is several times as great in the day as it is at night.

In Malaysia it is probable that nearly 100% of the vulnerable subimagos emerge in almost total darkness. Apparently the lowest predation rate of subimagos in the temperate regions also would be during hours of darkness. The selection pressure which seems to counteract selection for night-time emergence appears to be cool climate that slows transformation from the subimago to the imago. In the lowland tropics, nights are warm and most imagos which emerge in the first 1½ hours of darkness transform to the imago stage before 0300 h the next morning. At higher elevations, higher latitudes and in dry climates the contrast between daytime and night-time temperatures is greater, and this coupled with the lower average temperatures at higher latitudes and altitudes prolongs the temperature-dependent subimaginal stage. In the tropics it appears that most mayflies mate and lay eggs before noon, and most do so by 1030 h following their emergence the night before. Tjonneland (1970) states that in Uganda most Ephemeroptera (and Trichoptera) swarm between sunset and sunrise. If this statement is based on the arrival of imagos at light and the lack of observations on swarming at other times, it agrees with our observations in Malaysia. However, because it is not possible to see the swarms in the dark and because of swarming away from the stream the problem of when swarming occurs is rather complex.

The risk of predation is much lower per unit time in temperate regions and emergence of the subimago during full daylight occurs in many species. The most common time of emergence for most temperate species is from late afternoon through the first hour of darkness. In warm temperate regions with suitable night-time temperatures subimagos of various species may emerge during the night. The favored times of nuptial flight in tropical species are very different than in temperate species. The time of nuptial flight appears to be the result of selection to reduce the time of daylight exposure. With the favorable temperatures the mayflies have become imagos by daylight and swarming takes place from before dawn through the morning hours. Dusk appears to be the most common swarming time in temperate species. Table 1 compares my estimate of the most to least frequent times of swarming in tropical and temperate species.

Table 1.

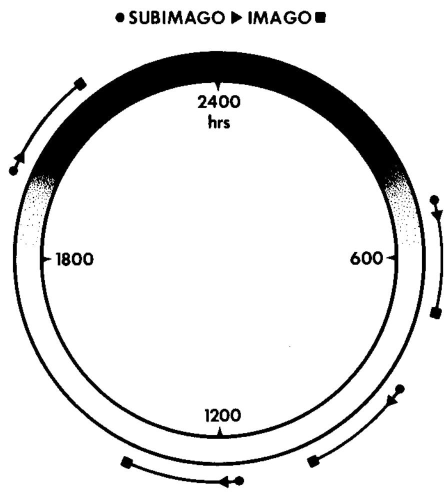
NUPTIAL FLIGHT TIME

Decreasing Frequency ↓	TROPICS	TEMPERATE
	Morning	Dusk
	First dark hours	Afternoon
	Dawn	Afternoon/Morning
	Midday	Morning
	Dusk	Midday
	Afternoon	Dawn
		First dark hours

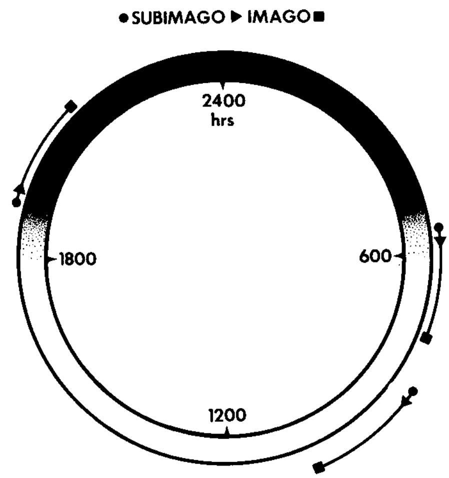
It is interesting to speculate that ancestral emergence and swarming habits may persist when mayflies disperse to new areas. For example, the emergence and swarming of *Tricorythodes* (Hall *et al.* 1975) and *Traverella* (Edmunds 1948) are basically tropical patterns and both appear to be extensions of South American genera into North America. In some cases, however, tropical forms in temperate regions presumably have shifted to temperate behaviour. *Dactylobaetis*, a genus of presumed South American origin, swarms in the evening in Idaho. The persistence of ancestral swarming patterns may account for the swarming of some Ephemerellidae and Heptageniidae in Sabah (Borneo) in early afternoon, but the area where such swarming was observed is at 1050 meters elevation. No afternoon or dusk swarming was observed at low elevations.

Eight to ten times the Ephemeroptera have evolved very short adult lives, in which the subimago stage lasts only for a few minutes, and the imagos live 2 hours or less; in some cases the female mates and dies as a subimago. This is true of all the Oligoneuriinae (and probably Chromarcyinae) (Oligoneuriidae), possibly in some Leptophlebiidae (*Isca)*, the known Behningiidae, some or all Euthyplociidae (*Proboscidoplocia, Polyplocia*), apparently all Polymitarcyidae, some or all Palingeniinae, some Tricorythidae (*Tricorythus* s. l., *Teloganella*), (*Teloganella* is a tricorythid, Edmunds in MS.), all Caenidae and in *Prosopistoma* (Prosopistomatidae). These short-lived mayflies are not subject to many of the mating flight time restraints imposed on species with longer lives, especially those with long-lived subimagos. Mating swarms of short-lived mayflies are crepuscular (e.g. *Ephoron)*, after dark (Euthyplociidae), pre-dawn or dawn (Behningiidae, *Prosopistoma,* some Caenidae) or in morning sunlight (some Caenidae). Swarming times of short-lived forms vary within a genus in the same general area; some species swarm in the morning while others are crepuscular, e.g.

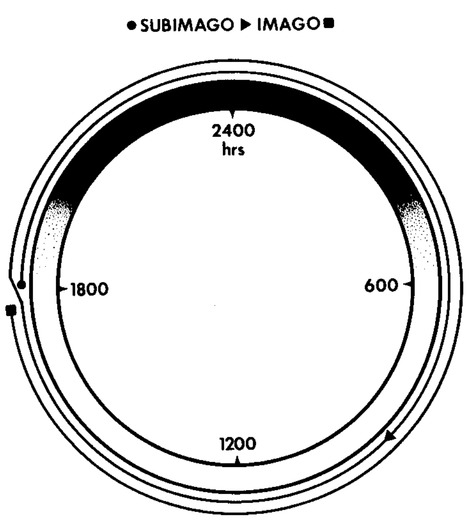
Figure 1. A generalized comparison of emergence and moulting to imago stages in specialized short adult life (<2 hours) and longer adult life (>6 hours) unspecialized species of Ephemeroptera in tropical and temperate regions. Specialized genera have the potential of being similar in the two regions, but nuptial flight in tropical regions is most frequently in the first hour of darkness. Unspecialized genera in the tropical lowlands tend to be strongly restrained to a short daylight life, although exceptions are known. In unspecialized genera of the temperate region, emergence of subimagos is scattered, and length of subimaginal and imaginal life is variable; the diagram indicates a common generalized pattern but does not show the range of variation.



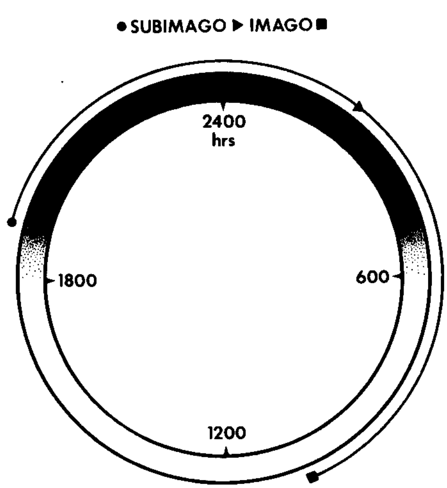
SPECIALIZED GENERA
TEMPERATE



SPECIALIZED GENERA
TROPICS



UNSPECIALIZED GENERA
TEMPERATE



UNSPECIALIZED GENERA
TROPICS

morning and evening swarming species of *Brachycercus* and *Caenis* or morning and midday swarming of *Lachlania*.

It is well known that many species of mayflies emerge seasonally. This occurs most frequently in temperate areas but appears to be true also of many tropical species. W.L. Peters (personal communication) noted a coordinated seasonal emergence of *Campylocia* in Peru. All known records of the adults of *Cheirogenesia decaryi* of Madagascar are February. Seasonal emergence results in greater concentration of adults at one time and increases the likelihood of mating success and tends to reduce the percentage of individuals taken by predation.

Mayflies also use water temperature, lunar cycles and possibly other environmental cues for coordinated mass emergence. Endogenous rhythms are also probable in some forms, e.g. *Dolania* (Peters and Peters 1977). Notable mass emergences have been reported in *Povilla, Campsurus, Ephoron, Eatonigenia, Hexagenia, Plethogenesia, Palingenia, Caenis, Oligoneuriella, Lachlania* and others. Mass emergence increases the probability of finding a mate and serves to satiate predators.

Remote nuptial flight is a common phenomenon in mayflies. We have frequently found nuptial swarms of *Baetis, Paraleptophlebia, Rhithrogena* and species of other genera at distances of 1.5 km from the nearest larval habitat. Probably many species whose nuptial flight has not been observed (e.g. some common species of *Ephemerella, Ameletus*, etc.) have nuptial swarming sites that are remote either laterally or vertically, high above the larval habitat. Remote nuptial swarming has energetic costs and increased danger of the female not finding her way back to the stream for oviposition. There is obviously some selection pressure against swarming over the stream, and we speculate that it is the higher concentration of predators near streams, rivers or lake margins.

We suspect that part of the explanation of the rarity of observations of swarming adults in Malaysia is because of remote nuptial flight. Corbet (1961) reported adults of *Adenophlebiodes burgeoni* swarming 6-10 feet above a 120 foot steel tower projecting above the forest canopy in Mpanga Forest, Uganda, Mass emergences that result in predator satiation obviate the streamside predation problem and it appears that all mass emergent species swarm over rivers (e.g. *Ephoron, Lachlania*) or river banks (e.g. *Traverella*).

Remote nuptial flight poses another problem; the mayflies must have some common orientation toward the remote swarm site. Many mayflies that swarm over or near rivers and streams orient to specific swarm markers: white water, slicks on the water, trees, shadows of trees or bushes, areas free of vegetation, and areas darker than the general background or lighter than the background. Each species is specific in its choice of swarm marker. Savolainen (1978) has given data on swarm markers for mayflies in Finland and W.L. Peters and the senior author gathered a substantial amount of data that remains unpublished. Remote nuptial flight seems to place a high premium on swarm markers and a reasonable prediction is that swarm marker orientation is an important aspect of remote swarming. Another facet of nuptial flight activity is timing; nuptial flight is most effective if both the place and time are restricted. In temperate mayflies, it is a combination of light and temperature that controls swarming time; in the lowland tropics, temperature would appear to be less restrictive and light intensity may be the prime environmental cue.

The importance of differences in emergence and swarming activities in different climates is obvious for those who are qualitatively sampling for Ephemeroptera in a region. The nuptial flight of adult *Prosopistoma* remained unknown until 1954 (Gillies 1954) primarily because the circadian rhythms of *Prosopistoma* and man did not coincide. In the Malay Peninsula and in Sabah, subimagos of Baetidae were first to emerge, just before full darkness, and were rapidly followed by species of a variety of other families. Emergence (as measured by arrival of subimagos at lights) declined markedly after one hour of darkness. In resuming collecting at lights at 0400 h large numbers of imagos of a variety of families appeared at lights, but very few subimagos. The specialized short-lived mayflies may emerge from larvae either in the first hour of darkness (e.g. *Polyplocia, Teloganella,* some Caenidae) or at dawn (*Prosopistoma,* some Caenidae) or during morning (*Isca*) but most long-lived species emerge in the first hour of darkness, transform to adults by dawn, and mate in the morning (Fig. 1). In Malaysia, most of the species that were subimagos in the first hour of darkness were collected as imagos in the morning and many species not seen the night before were collected. Between 0700 and 0715 h two females of *Prosopistoma* came to the mercury vapor light. Some short-lived species, however, were collected only by collecting just after it became dark. In Malaysia, it appears that subimagos of *Potamanthodes* and *Rhoenanthus* (Potamanthidae) do not transform the first night, but no other exceptions were noted.

The use of a light in Malaysia at dusk and the early hours of darkness resulted in imagos of specialized short-lived species and in many subimagos that had to be placed in subimago boxes until emergence of the imago. By using lights before dawn the specimens collected were imagos and much time was saved. It is now overwhelmingly clear that the adult mayflies of the tropical lowlands will become well known only by collecting after dusk and before dawn. This appears to be equally true of Trichoptera, Plecoptera and other insect groups.

RESUME

La vie brève des éphéméroptères adultes est une espèce d'adaptation propre à ces insectes pour réduire au minimum le temps où ils sont sujets à être victimes des prédateurs. La vie d'adulte de huit à dix familles à évolution indépendante et à morphologie complète ne dure que deux heures tout au plus. Les Odonates et les oiseaux prédateurs sont particulièrement voraces dans les basses-terres tropicales, et la plupart des formes non-différenciées à durée de vie plus longue émergent au stade de subimago dès les deux premières heures d'obscurité, passent au stade d'imago avant l'aube, s'accouplent et pondent leurs oeufs vers le milieu de l'avant-midi. Dans les régions tempérées, les nuits fraîches s'opposent souvent au processus de développement propre aux régions tropicales. En outre, le fait qu'il y ait moins de prédateurs rend possibles d'autres modes d'évolution. C'est ainsi que les éphéméroptères des climats tempérés ont des périodes d'émergence et d'essaimage variées. Les éphéméroptères à vie brève sont sujets à moins de contraintes aux périodes d'émergence et d'essaimage et leur morphologie tropicale ressemble à leur morphologie des régions tempérées. L'émergence saisonnière et leur émergence quasi-simultanée en masse sont des mécanismes destinés à rassassier les prédateurs. Les vols nuptiaux vers de lointaines destinations se sont probablement présentés comme une stratégie pour échapper aux prédateurs, et l'on suppose que pour s'envoler au loin les essaims ont dû nécessairement suivre des guides. Il est probable qu'il est plus commun de trouver des guides chez les éphéméroptères tropicales que chez celles des régions tempérées. Il semble enfin qu'en se dispersant sur de nouveaux territoires, les éphéméroptères conservent certaines habitudes ancestrales d'émergence et d'essaimage.

ZUSSAMENFASSUNG

Die Abkürzung des Erwachsenenlebens von Ephemeroptera stellt eine Adaption dar zum Zwecke der Verringerung der Zeit während der die Tiere Prädatoren ausgesetzt sind. Bei acht bis zehn spezialisierten Stämmen ist das Leben ausgewachsener Fliegen auf zwei Stunden oder weniger reduziert. Die Prädation durch Odonata und Vögel ist besonders intensiv in tropischen tiefgelegenen Gegenden. Die meisten länger lebenden Formen treten in den ersten beiden Stunden der Dunkelheit als Subimagos zutage, verwandeln sich vor der Morgendämmerung in Imagos, paaren sich und legen Eier im Laufe eines Vormittages. Dieses tropische Verhaltensmuster wird aber in gemäßigten Gegenden oft durch kühle Nachttemperaturen verhindert; auch bildet sich ein anderes Verhaltensmuster wenn verringerte Prädation besteht. Eintagsfliegen in gemäßigten Zonen haben daher verschiedene Emergenz- und Schwärmzeiten. Kurzlebige, spezialisierte Gattungen sind nicht so vielen Einschränkungen

bezüglich Emergenz- und Schwärmzeiten unterworfen. Auch sind sich tropische Formen und solche von gemäßigten Zonen sehr ähnlich. Saison Emergenz und koordinierte Massenemergenz sind Mechanismen zur Sättigung der Prädatoren. Der entfernte Hochzeitsflug entstand wahrscheinlich als Mechanismus gegen die Prädatoren. Man nimmt an, daß Schwärmanzeiger wesentlich sind zur Ermöglichung des entfernten Fluges. Es ist denkbar, daß Schwärmanzeiger häufiger bei tropischen Eintagsfliegen auftreten als bei solchen der gemäßigten Zonen. Es gibt Beweise dafür, daß angestammte Emergenz und Schwärmgewohnheiten bestehen bleiden, wenn Eintagsfliegen sich auf neue Gebiete verbreiten.

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