Behavioural strategies of emergence, swarming, mating and oviposition in mayflies

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Abstract. Behavioural strategies of emergence, swarming, mating and oviposition in mayflies are reviewed in the light of available literature.

1. Introduction

Mayflies are unique among the insects in having two winged adult stages, the subimago and the imago. The adults live from 1–2 hr to a few days and even up to 14 days in some ovoviviparous species. The brevity of the adult stage is possible because the sole function of the adult is to reproduce. In fact, the process of natural selection has resulted in insects whose every adaptation is directed towards the process of reproduction. Moreover, the abbreviated adult life of Ephemeroptera is an adaptation to minimise exposure time to predators (Edmunds and Edmunds 1980). An attempt is made to review the data on behavioural strategies of emergence, swarming, mating and oviposition in mayflies.

2. Emergence

Emergence, the transition from the aquatic nymph to the terrestrial subimago, is a critical period for mayflies. Shedding of the nymphal skin usually occurs at the water surface on some object such as a stone or macrophyte stem or in mid-water (Brittain 1982). The latter is more typical of the burrowing species which inhabit deeper waters, and of a number of river species. Genera such as *Siphlonurus*, *Isonychia* and *Baetisca* crawl completely out of the water before they moult (Edmunds *et al* 1976). The mechanism of emergence has been well documented in *Baetisca rogersi* (Pescador and Peters 1974). The emergence process begins with a medial split of the thoracic notal shield. The abdominal segments contract repeatedly in a peristalic fashion followed by the outward bulging of the thorax until the entire medial line of the mesothoracic notal shield opens. The split gradually progresses anteriorly and posteriorly. Anteriorly it reaches the vertex of the head, usually between the compound eyes along the obscured ecdysial line, but sometimes extend to the base of the frontal process of the head. Posteriorly the split terminates at the posterior margin of the median carina. As the split progresses, the subimago wriggles out from the old skin. The dorsum of the subimaginal thorax emerges first, followed by the compound eyes and then the head. At this point the emerging subimago assumes a slanted position with the head and anterior

half of the thorax completely exposed, and the abdomen still encased in the old cuticle. Quick jerky body movements and abdominal contractions complete the process with the release of the abdominal segments and caudal filaments. Sometimes the subimago spreads out its prothoracic legs immediately upon exposure and firmly anchors the claws on the supporting objects. This probably helps the emerging subimago pull itself from the nymphal skin. Normally the prothoracic legs and the mesothoracic legs remain firmly drawn under the venter of the thorax until the metathoracic legs appear and all three pairs spread out at the same time. At emergence the wings of the subimago are moist and are often curled at the apex. A newly emerged subimago remains motionless for a while, and then crawls up on the supporting object. This resting behaviour probably allows the subimago time to regain its strength and dry its wings (Pescador and Peters 1974).

Mayfly emergence patterns can be analysed under two categories:

2.1   Diel patterns

Edmunds and Edmunds (1980) makes an interesting comparison of emergence in specialized short life (< 2 hr) and longer adult life (> 6 hr) unspecialized species of Ephemeroptera in tropical and temperate regions (figure 1). Specialized genera have the potential of being similar in the two regions. For example, the emergence of the short-lived Caenidae invariably takes place either at dawn or dusk and appears to be
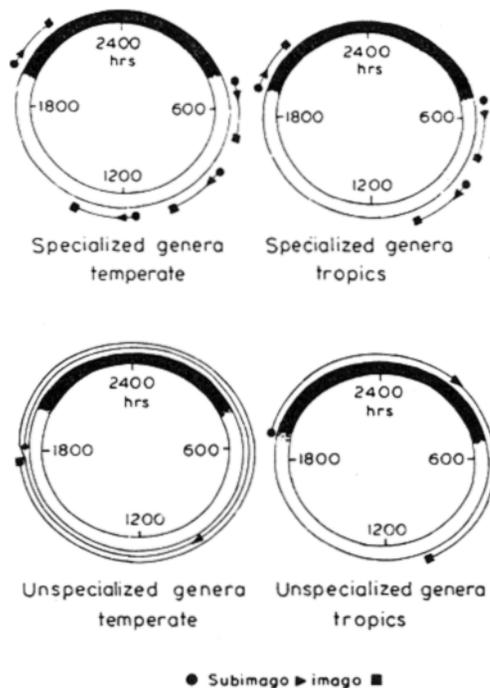

Figure 1. A generalized comparison of emergence and moulting to imago stages in specialized and unspecialized species of Ephemeroptera in tropical and temperate regions (after Edmunds and Edmunds 1980).

controlled by light intensity (Muller–Liebenau 1960). On the other hand, whereas in the unspecialized genera of the temperate region, emergence of subimagos is scattered, and length of subimaginal and imaginal life is variable, unspecialized genera in the tropical lowlands tend to be strongly restrained to a short daylight life, although exceptions are known (Edmunds and Edmunds 1980). Furthermore, nearly 100 % of the vulnerable subimagos emerge in almost total darkness in tropical lowlands whereas emergence of the subimago during full daylight occurs in many temperate 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.

Edmunds and Edmunds (1980) point out that 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. Apparently the most significant daytime predators in tropics are Odonata. Birds are secondary. Most mayflies are killed also in spider webs. The only significant night time predators are bats. It is also clear that predation on mayfly subimagos and imagos is several times as great in the day as it is at night. Apparently the lowest predation rate of subimagos in the temperate regions also would be during hours of darkness. However, 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 $1\frac{1}{2}$ hours of darkness transform to the imago stage before 0300 hr the next morning.

2.2 Seasonal patterns

Mayflies have distinct and finite emergence periods, especially in temperate and arctic areas. In cold temperate and arctic areas, mayfly emergence is more or less restricted to the summer months, owing to the physical barrier of ice cover and the low air temperatures during the rest of the year (Boerger and Clifford 1975; Brittain 1982; Ulfstrand 1969). Probably only a few species such as *Baetis macani* are able to emerge at water temperatures below 7°C (Brittain 1975). As one approaches the tropics, and also in more oceanic climates, there are fewer restrictions and emergence may occur throughout much of the year, although most emergence still occurs during the warmer months (Clifford 1981). In the tropics emergence is often non-seasonal, (Tjonneland 1960, 1970), although some species have clear emergence patterns. The lunar rhythm of emergence of the African species, *Povilla adusta*, is well known from a number of lakes (Hartland–Rowe 1958).

In habits with several mayfly species, peak emergence of the major species may be separated in time, especially in congeneric species (Brittain 1982). Such temporal separation over the emergence season may serve to reproductively separate species (Friesen *et al* 1980). Recent authors who have studied emergence 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 endogenous rhythms (Corbet 1964; Humpesch 1971; Thibault 1971; Fremling 1973 a, b; Langford 1975; Peters and Peters 1977). In species with well defined emergence periods, males and females usually emerge synchronously, which may ensure survival of adequate numbers of organisms for successful reproduction (Friesen *et al* 1980). Emergence should be viewed as an integral part of the species' overall life cycle strategy (Brittain 1980).

3. Swarming and mating

Swarming is a male activity, apart from the Caenidae and Tricorythidae where both males and females may participate. The females fly into these swarms and mating occurs almost immediately and usually in flight. The flight of mayflies is a sort of wedding dance. Swarming may take place over the water itself, over the shore area, or even remote from the water. For instance, the swarms of *Baetis, Paraleptophlebia* and *Rhithrogena* have been observed up to several kilometers from the nymphal habitat (Edmunds and Edmunds 1980). Most swarms are oriented according to terrain markers such as areas of vegetation, the shoreline, and trees (Savolainen 1978). The time of swarming varies considerably, although dusk is the most common time of the day in temperate areas. Light intensity and temperature are major factors in determining the timing of swarming. The time of nuptial flight appears to be the result of selection to reduce the time of daylight. Table 1 is the estimate of Edmunds and Edmunds (1980) regarding the most to least frequent times of swarming in tropical and temperate species.

The behavioural adaptations for mating as evident in the shape and location of eyes, and foreleg modifications in males are really striking. The prominent turbinate eyes of males, especially well-developed in the Baetidae and some Leptophlebiidae, provide both high acuity and good sensitivity (Horridge 1976). This enables them to detect and capture single females in a swarm at low light intensities. The forelegs of male are unusually long for grasping and holding the female during mating. The other legs are reduced. The backward bent of tarsus necessary for the suspension during mating is made possible by a reversible joint at their bases.

Brinck (1956) observed mating in *Parameletus chelifer*. Males dominate during the early swarming period. But soon numerous females mixed with the swarms. The male pressed himself under the female abdomen and stretched the front legs forwards and upwards along the sides of her body, until they reached the prothorax. Then the tarsus

Table 1. Nuptial flight time (after Edmunds and Edmunds 1980).

	Tropics	Temperate
Decreasing frequency ↓	Morning	Dusk
	First dark hours	Afternoon
	Dawn	Afternoon/Morning
	Midday	Morning
	Dusk	Midday
	Afternoon	Dawn
		First dark hours

were bent so that each clasped round a wing-base. At the same time the abdomen was curved and the forceps grasped the 8th or 9th abdominal segment of the female. The female abdomen was usually held like an S so that the penis was easily pressed into the female genital opening. The male cerci were stretched forward, fixing the female abdomen at the same vertical plane as the male abdomen. The female cerci were directed obliquely hindward (figures 2 A,B). The copulation lasted about 20 sec and then the male took off, soon followed by the female.

The suspension of the male body in the anterior legs and the forceps is certainly very safe. It is most probable that the above type of male suspension in anterior tarsus and forceps is characteristic of this insect group. This is indicated by the presence of the forceps in all males investigated and lengthened male front legs in all species known.

4. Oviposition

Specialized structure like ovipostor found in other groups of insects, is lacking in mayflies. However some authors call the produced subgenital plate an ovipositor. We prefer to call it 'egg channel' (Sivaramakrishnan 1984). The problem of downward displacement of eggs and immature nymphs, can be compensated for by the adult mayflies flying upstream before they lay eggs.

Oviposition behaviour of mayflies can be categorized under five basic types (Elliott and Humpesch, Personal communication).

(i) *Female goes underwater and eggs laid on substratum:*
Baetis rhodani belongs to this category (Elliott 1972). The female lands on a partially submerged stone in rapidly flowing water, folds her wings along the abdomen, then walks under the water and searches for a suitable oviposition site, usually on the
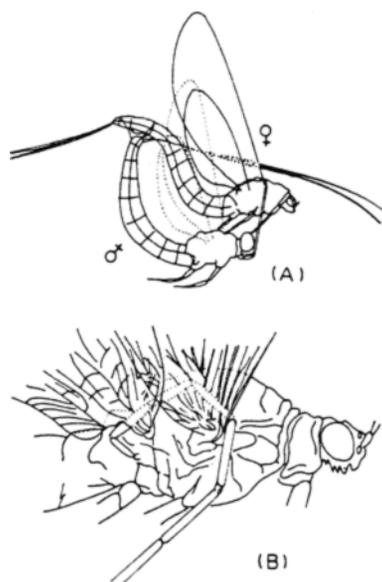

Figure 2. *Parameletus chelifer* Bengts (after Brinck 1957) A. Mating couple in flight. B. The backward bent of the tarsus of male clasped round the wingbase of female.

underside of the stone. This behaviour may permit assessment of water quality before oviposition (Sutcliffe and Carrick 1973). The female lays contiguous rows of eggs to form a flat semi-circular plate. When oviposition ceases, the female may walk out of the water and fly away, but she is usually swept away downstream.

(ii) *Female rests on a stone above water and eggs laid on substratum under water:* *Habroleptoides modesta* (Pleskot 1953) belongs to this category in which the female dips its abdomen in the water and lays eggs. The female is never totally submerged. The tails are usually broken off before oviposition starts.

(iii) *Female flies down to the water surface and eggs are released in a single mass:* In *Ephemerella ignita* (Elliott 1978) the egg mass forms a spherical greenish ball that is carried at the genital aperture with the posterior abdominal segments curved downwards and round the ball to hold it in position. The female flies upstream and descends to the water surface, releasing the egg-ball on contact with the water.

(iv) *Female flies down to the water surface and eggs are released in several batches:* In *Rhithrogena semicolorata* (Humpesch and Elliott 1980) the female flies upstream, descends to the surface of the water and releases a few eggs by dipping the tip of her abdomen at intervals. Most species belong to this category.

(v) *Ovoviviparous species:* *Cloeon dipterum* is the only species in which the females rest for 10–14 days after copulation and then lay their eggs on the surface of the water. As soon as the eggs come into contact with the water, they hatch and the larvae swim away (Degrange 1959).

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