

Confusing Behaviour

Peter Barnard, entomologist from The Natural History Museum, discusses how swarming is an essential part of the riverfly life-cycle and why understanding this behaviour, which may be confused with hatching, is important to the angler.

Swarms of riverflies are a common sight near rivers. These swarms appear to have a constant shape and position but close inspection reveals that they consist of hundreds or thousands of individuals flying in dance-like vertical or horizontal patterns.

To most people the word swarm conjures up the rather vague idea of a congregation of insects, all flying close together, either forming a stationary cloud or else flying in a purposeful way in a constant direction; this concept agrees with most dictionary definitions. Bees and locusts are the insects that usually come to mind, but anyone who has spent time near lakes or rivers will have noticed swarms of riverflies, such as the upwinged flies or mayflies (Ephemeroptera), the caddisflies (Trichoptera), the stoneflies (Plecoptera) and some of the two-winged flies (Diptera).

Bees form a swarm when they are following a queen bee to a new nest-site, and locusts migrate in enormous numbers, often over great distances, to find new food sources or better habitats. But these are both examples of moving swarms, so what are the more stationary swarms of riverflies actually for?

Riverfly life-cycles

To understand this, we need to look at the function of each stage of the insect life-cycle.

The eggs of riverflies are nearly always laid

directly in the water; the larvae or nymphs that hatch from the eggs form the main feeding stage in the life-cycle. Whether an active predator or a grazing herbivore, the larva is the only stage in the life-cycle that can build up food reserves and grow to many times its original size by moulting several times. When fully grown, the larva has to change into the adult form and the more advanced insect groups pass through a pupal stage to make this drastic metamorphosis a little easier.

Adult upwinged flies and stoneflies are similar to their larvae with the addition of wings and longer antennae. Adult caddisflies are completely different from their larvae. During the pupal stage of the caddis, which usually takes place in a shelter of some kind, there are changes to external features and the internal organs are re-arranged into their adult form. The pupae of all riverflies eventually make their way to the surface of the water and adult flies emerge.

The first obvious difference between the adult flies and the pupae is that the adults can fly a considerable distance, enabling them to colonise new sites. Eggs can only drift in the current, larvae do not usually travel far in running water in case they are swept away downstream and the transitional pupae swim straight up to the surface: none of these younger stages can disperse the species into

suitable new habitats. Many flies that live in running water fly upstream before laying their eggs so as to counteract the tendency of their eggs and larvae to drift downstream: without this correcting behaviour fly populations would end up in the sea!

But the main function of the adult stage is reproduction, preferably with mating enabling the mixing of genetic material to ensure the future of a healthy population.

The mating swarm

Swarming in riverflies is linked entirely to successful mating. The apparently aimless activity of flying around, but going nowhere, actually is time well spent. Flight uses up a lot of energy and insects fly for all kinds of reasons. For groups like dragonflies it is often to catch prey. This is not the case for most riverflies as they do not feed in the adult stage. So in those flies that cannot renew their energy reserves, flight is parsimoniously used for essential activities such as emergence (hatching), mating, dispersing and egg-laying. Adult caddisflies can imbibe some liquid food and so live longer, which means they can afford to wait for suitable weather conditions before reproducing, but upwinged flies cannot feed and so cannot wait too long before mating and laying their eggs.

The upwinged flies, or Ephemeroptera, are perhaps the most familiar of the swarming riverflies. Their swarms initially consist entirely of males, numbering hundreds or even thousands; careful observation shows that each individual may be flying in dance-like vertical patterns or horizontal lines, depending on the species. Regardless of individual flight paths the swarm maintains a relatively constant shape and position, but this is not because the flies are aware of each other and are acting gregariously. They are all responding to the same external stimulus, behaviour also shown by a flock of starlings or a shoal of fish. For riverflies this stimulus often is a visual marker such as a bankside tree or a human observer; it is possible to walk slowly along the river-bank being followed at a fixed distance by the swarm of insects.

Most stoneflies are not strong fliers and do not form mating swarms, but the non-biting midges (Chironomidae) or "buzzers" may fly in swarms of many thousands of flies that, from a distance, can look like clouds of smoke.

The females appear

The constant darting around of the males within the swarm means that they can keep a lookout for females that are attracted into the edge of the swarm: if a male stays in the centre he will have little chance of finding a mate. Before the swarm actually forms, the females have been sitting around on nearby vegetation, conserving their energy, but the presence of the male swarm stimulates the females to fly into it, where they are rapidly grabbed in mid-flight by the males. Many upwinged flies have modified eyes, with larger facets in the top half, which make the task of spotting females easier. This reaches an extreme in the family Baetidae (which includes the olives and spurwings) where the males have a turret-like vertical extension on their eyes. These "turbinate" eyes enable the male to fly underneath the female and grab her from beneath with his long front legs. Even in the caddisflies it is common for the males to have larger eyes than the females,

but despite this they often make mistakes, either grabbing another male or even an individual of the wrong species. But in these cases the mistake is realised quickly, because the female produces a unique scent, called a pheromone, which is both a sex-attractant to males of her own species and an aphrodisiac to ensure that successful mating takes place. The characteristic zig-zag flight of some caddisflies is designed to sniff out the pheromones emanating from receptive females. The act of mating may occur in mid-flight, but often the couple fly to nearby vegetation to finish the process. The male may be able to mate again, but the female will prepare to lay her eggs.

Swarming and the hatch

Having established that swarming is an essential part of the reproductive behaviour of riverflies, does this have any significance for the angler? Some angling authors are quite dogmatic about the daily timings of insect hatches or emergence of adults from the water surface, but it is likely that some of these statements apply more to swarming activity than to emergence. Many species, such as the longhorn caddisflies, swarm in the late afternoon or evening when the timing probably is triggered by changes in light intensity; most species cannot maintain swarms in strong winds, because their flight is too weak, nor do they fly in cold weather. Synchronised emergence is common, but it is not the same as swarming.

But if large numbers of flying insects are present, does it matter to the fish and hence to the fisherman? Yes, because it is important to understand the behaviour of the flies. Some emerging species are very vulnerable to predation by fish, especially when they struggle on the surface before flying. Some caddisfly pupae swim rapidly and strongly to the shore, but this conspicuous activity is attractive to fish. So hatching is a precarious time for flies.

After mating, most female flies lay their eggs directly in the water or on suitable vegetation. The exhausted spent flies often die on the water, again attracting much attention from hungry fish. But swarming is a strictly aerial activity, during which flies may land on the ground or bankside vegetation but not on the water, so the sight of large insect swarms does not necessarily tell us what the fish are feeding on. Emergence and oviposition attract the attention of fish, but swarming does not do so.

So look carefully at books that describe the hatching times of insects, they may be describing swarming, rather than emerging. Large numbers on the wing do not necessarily mean a hatch; there is no substitute for your own careful observation!

Dr Peter Barnard is a specialist on caddisflies and runs the British Insect Research Programme at The Natural History Museum in London. He is currently writing a handbook on the adult British caddisflies and is a contributor to the collaborative Riverfly Workshops that are targeted towards individuals keen to identify and monitor the riverfly life on their stretches of water.

Peter can be contacted at: Entomology Department, The Natural History Museum, Cromwell Road, London SW7 5BD. Email: P.Barnard@nhm.ac.uk