***What to do next?*** First I decided I would not be fulfilled doing non-invasive behavioural experiments — I need to go into the brain to be happy. I could have chosen computational work but I am an experimentalist at heart. Having that decided, the question was then which species? Where and how was I going to set my new boundary, a personal and arbitrary line without scientific grounding? This process was quite refreshing as everything was open again, like when you are choosing your PhD.

After thinking about it for quite some time, and having gone through non-model versus model organisms, I finally decided to move to fruitflies. I feel that *Drosophila* neuroscience is at an exciting stage, with an ever increasing number of interesting behavioural paradigms and amazing tools to dissect their underlying circuits. My plan is to study how the social environment affects defense behaviours in flies. I wonder if or how long will it take me to re-define my boundaries again, launching me into yet another research path.

***What is the best advice you've been given?*** Three come to mind. The first is a great piece of advice Tad Blair gave me, which I make a strong effort to follow, which was to always stay close to the data.

The second, rather technical, but given with a tone of mysterious wisdom, came one day at a Society for Neuroscience meeting, while walking through the poster aisle on place cell recordings I asked Matt Wilson how people managed to record from so many cells (a mission at which I was failing miserably). He told me "don't go to the cells, let them come to you", meaning when moving down the electrodes the brain gets pushed down, so if one stops the electrodes before reaching the final recording site, the brain will relax back to its position and the electrode will end up in the right place.

Third and last is a piece of advice I have received often, but make an effort *not* to follow, which is to focus my research scope on a narrower set of questions.

***What is your greatest research ambition?*** I have a mental block anytime I am asked what is *the* most important question to be answered in my field. Having given up on the ability to identify these important questions, I will keep on being driven by questions that spark my curiosity. I hope someday the community in my field may deem one of these questions as important. I would also be really happy if my scientific path turns out to have helped other people become better scientists.

***What do you think are the biggest problems science as a whole is facing today?*** In discussions centred on how to make science better, too often the scientists leave themselves out of the equation. This is particularly relevant now, as we face a disproportional growth of the scientific community relative to its resources. We have a pyramidal structure that is asphyxiating young scientists, which leads to intense competition and many times de-humanizing practices. One can discuss whether competition is good for scientific progress, but what is best for the advancement of scientific knowledge is not always best for the scientists. I strongly believe that the ends (scientific progress) do not justify the means (pressure on scientists) and thus feel we should be careful not to forget this distinction.

***If you could ask an omniscient higher being one scientific question, what would it be and why?*** I would ask if we decide when to stop fighting to live and if so how does the brain command the shutting off of our body and itself. There is ample anecdotal evidence that humans and other animals either know or decide when the end of the line has been or is to be reached. These suggest that staying alive in limit conditions (either by age, disease or injury) results from an active process of survival, and that at some point something changes, this process is switched off and death occurs. This switch is most likely or most often not deliberate. Still, I find it fascinating that the brain may actually control our body to such an extent as determining life and death.

Behavioral Neuroscience Lab, Champalimaud Neuroscience Programme at Instituto Gulbenkian de Ciência, Oeiras, Portugal.
E-mail: marta.moita@neuro.fchampalimaud.org

Quick guide

# Flying insect swarms

Ian A.N. Dublon[1] and David J.T. Sumpter[2,*]

***Which insects swarm and why?*** Flying insect swarms come in many different shapes and sizes. Some, such as the crop-eating locust swarms or the mating swarms of disease-spreading mosquitoes, are thought of as pests. Others are beneficial to our ecosystem, such as honeybee swarms and migrating butterflies. There are also many swarming species, such as midges, dance flies, mayflies and thrips, that are commonly observed, but less well studied.

Flying swarms are usually either mating or migrating. Stationary mating swarms form over a specific substrate or 'marker'. In mosquitoes, males aggregate first and then the females arrive one by one. Interactions involve visual and auditory cues, but the ultimate result of these interactions is the same. Pairs form and depart for in-flight copulation. In some cases, such as mayflies, lovebugs and ants, the male mating swarms move together to sites of female emergence or feeding. Chemicals can play an essential role in swarm orientations. On spring evenings, female cockchafers (*Melolontha melolontha*) release sex pheromone when feeding. Male swarms home in on the combination of pheromone and specific green leaf volatiles elevated during plant damage. These mating migrations are on a relatively small scale compared to the vast migratory swarms formed by locusts, or even butterflies. In these swarms the group moves together looking for food and/or shelter.

***What are the most spectacular examples?*** Grasshoppers win on sheer size and scale. In May 2014, the US National Weather Service detected swarms of grasshoppers flying over 300 m above Albuquerque. The swarm was so large, covering the entire city, that the weather service initially assumed that it was a weather front. Only when they saw that the 'particles' moved in a non-random way did they realize it must be grasshoppers. These images probably provide some of the best estimates of the size of flying swarms. Historic reports of African locust swarms are unreliable because of measurement difficulties, but according to Uvarov's classic text, locust swarms can cover up to 1000 km$^2$.

Honeybee swarms may win in terms of collective intelligence. Around 50 to 100 scout bees lead swarms consisting of thousands of workers and a queen to a new nest site. The scout bees co-ordinate the swarm by flying rapidly or 'streaking' through the swarm in the direction of the new home. Butterflies make somewhat less frenetic migrations in advance of periods of cold weather. The most famous is the monarch butterfly (*Danaus plexippus*). In late summer or early autumn, this insect utilises tailwinds to travel over 3500 km over around 75 days. The butterflies rest in overnight clusters within trees. In the morning, they either resume if the prevailing wind is agreeable, or search for nectar if it is not. The methods used to maintain this migratory flight course are unclear, though geomagnetism and polarised light orientation have been proposed.

Although stationary, midges and mosquitoes shouldn't be underestimated. In March 2014, photographer Filipa Scarpa captured a mosquito tornado on camera (Figure 1). Such a column-like shape is rare, but it isn't unusual for non-biting midges, such as lake flies, to form vast swarms. Dance flies form smaller spherical shapes, which make spontaneous shifts in position. Within the space of a few seconds the whole swarm will relocate a metre either up or down. Inside these swarms the flies engage in intensive assessment of partner quality. In the dance fly species *Empis borealis* it is the females that aggregate and a single male enters the swarm carrying a nuptial gift, in the form of protein rich food. He inspects the hovering females, and when he has chosen a partner, he delivers the gift and the couple mates (Figure 2).

Mating swarms can also be remarkable in the brevity of their lifetime. The mayfly, which belongs to the aptly named Ephemeroptera order, presents a phenomenal display of mass copulation for only a few hours after emergence. Stationary swarming can be observed over or near water and shorelines on warm summer evenings. Swarm size and height is species dependent, though the swarm itself can be both low flying and broad, containing up to 200 individuals. These are medium sized insects, so any swarm is hard to ignore. Indeed, the swarming can go spectacularly wrong if, as is sometimes the case, the swarm uses a busy asphalt road as a marker.

***What can we measure inside swarms?*** During the last year, several different research groups have independently tackled the problem of quantifying the structure of midge and mosquito swarms. Techniques, first developed by physicists to study starling flocks, have been used to reconstruct the three-dimensional trajectories of individuals. Analysis of these data has revealed patterns in the flight paths of individuals. For example, male midges show ballistic motion, flying straight through the swarm, but turning abruptly when they reach its outer edge. Similar analysis has revealed patterns of interactions between individuals. Male mosquitos fly through the swarm in parallel pairs. Midges also cluster together within the swarm, with small distances between nearest neighbours.

Migrating swarms can be studied in a similar manner. By placing cameras under a moving honey bee swarm, engineers have been able to identify the fast moving streaker bees. The streakers were located at the top of the swarm. These bees first perform high up streaks to guide the swarm and then return, possibly through the loosely organised lower part of the swarm, in order to lead further streaks. These results help explain how small numbers of scout bees can guide large swarms to a new nesting site.

***What has physics got to do with insect swarms?*** It may seem strange that physicists and engineers have invested so much time tracking and measuring correlations in midge swarms. Their interest in midges can be best understood if we think of insects as particles. This analogy leads to the intriguing possibility that insect swarms can undergo phase transitions, from a disordered gas-like state to an ordered liquid-like migration. As in physical systems,

Figure 1. A mosquito 'tornado' in Leziria Grande at Vila Franca de Xira, near Lisbon, Portugal. Copyright: Filipa Scarpa.

these transitions occur suddenly as swarm density passes a critical point.

In their recent study, Attanasi *et al*. [2014] found that midge swarms are just below the critical point of phase transition. Although the swarm does not move collectively, as it would if it were above the transition point, it exhibits medium-scale correlations within the group. These correlations are caused by waves of motion, where parts of the swarm move together for short periods of time. It isn't clear why the correlations have evolved. One possibility is that they are related to competition for females. A male can use the movement of others to detect whether a female is passing through another part of the swarm. When no females are present, the males chase each other around, unable to separate signal from noise.

While mosquitos can be thought of as a sub-critical gas, gregarious locust swarms can be thought of as passing the critical point for collective migration. Stronger interactions and higher densities cause the swarm to move in a common direction.

***Where to now?*** The mosquito is often labelled as the world's most deadly animal, because of its role as a vector of malaria. Identifying ways of reducing mosquito numbers or its efficiency as a vector may prove the key to eliminating malaria. Some potential methods rely on introducing sterile or genetically modified males into the population. By understanding how males compete within swarms,

Figure 2. Dance flies, *Empis borealis*, mating after the male has presented a prey for the female to eat. Svanemosen, Kolding, Denmark. Copyright: Erland Refling Nielsen.

it may be possible to increase the mating success of these genetically modified males. For example, a genetic line of males that respond more rapidly to their neighbours may be able to pick up more quickly on mating opportunities than their competitors. Care will be needed in introducing any such mutation. If interactions become too strong within a swarm there is a danger it will start to migrate collectively, allowing it to spread itself and potential disease still further.

Our questions about mosquito swarms are an example of a general question about how individual interactions are integrated to produce the swarm as a whole. Studies at the individual level have revealed a rich diversity of audio, visual and chemical cues and signals. Mosquitoes can hear and respond to each other's flight tones. In the southern house mosquito, male–female coupling occurs with wing-beat frequencies converging on the nearest shared harmonic. In insects with developed vision there is continuous optical feedback whilst flying. For example, locusts thrust forward when they perceive regressive motion, ensuring that the swarm doesn't leave them behind. Optic flow feedback can even be utilised in near darkness, as demonstrated in the nocturnal sweat bee. Pheromones emitted by honeybee queens attract flying drone swarms over 100s of metres, while other species may use pheromones to keep the swarm together.

The challenge for the future is to map from individual interactions up to the shape and dynamics of the swarm and then to measure the impact of the swarms at an ecological level. Locusts, honeybees, butterflies and mosquitos are all, for various reasons, key players in our environment. An interdisciplinary approach, involving engineers, physicists, chemists as well as biologists, is essential to establishing how flying insect swarms work at these different levels.

### *Where can I find out more?*


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[1]Biodiversity Research Centre, Earth and Life Institute, Université Catholique de Louvain (UCL), 1348 Louvain-la-Neuve, Belgium.
[2]Mathematics Department, Uppsala University, Box 480 751 06, Uppsala, Sweden.
*E-mail: david.sumpter@math.uu.se