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Quick guides

Murmurations

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What do you call a group of starlings? Collections of animals have been given some of the most fanciful, and sometimes unusual, nouns. Therefore, it is little surprise that "What do you call a group of ...?" is one of the first questions asked of scientists studying collective animal behaviour. Tuneful finches are known as a *charm*, whilst corvids do less well: collections of crows and ravens are known as a *murder* or an *unkindness*, respectively. One of the most stunning examples of collective behaviour is the spectacular display of European starlings (*Sturnus vulgaris*), the noun for which is a *murmuration* (Figure 1). These nouns are useful in evoking the powerful imagery of moving animal groups, and enliven the often-dense scientific publications produced by biologists, engineers, physicists and mathematicians on the topic. Given the richness of collective nouns and the recent surge of interest in the mechanisms and evolution of collective behaviour, it is perhaps ironic that there is no agreed collective noun for the different types of moving swarms, schools, flocks, herds and murmurations. Usually scientists studying these systems content themselves with saying that they are studying examples of *collective motion.*

Where can I see a murmuration? The mesmerizing act is typically seen at dusk throughout Europe, between November and February. Each evening, shortly before sunset, starlings can be seen performing breathtaking aerial manoeuvres, before choosing a place to roost for the night. These range in number from a few hundred to tens of thousands of birds. Murmurations exhibit strong spatial coherence and show extremely synchronized manoeuvres, which seem to occur spontaneously, or in response to an approaching threat, like hawks or peregrine falcons.

Figure 1. A spectacular murmuration of starlings. Photo: courtesy of ISC-CNR, Starflag Project.

According to the Royal Society for the Protection of Birds (RSPB) in the UK, starling numbers have been falling across northern Europe and the UK since the early 1980s, but the cause of the starling decline in the UK is unknown. Nonetheless, massive murmurations can still be seen in the UK. Other passerine birds also form large gatherings at dusk before settling down at a communal roosting over the winter months. For example, sightings of several thousand rooks (*Corvus frugilegus*) or jackdaws (*Coloeus monedula*) are not uncommon. Although not quite as manoeuvrable as starlings, their sheer number and noisiness are no less impressive.

Why do murmurations occur? The short answer is that we really do not know. However, there are a number of different theories, most of which centre upon managing predation risk. The larger group you are in, the better the chance someone else will get eaten if a predator attacks. This idea, known as the selfish herd, is a favourite explanation in undergraduate evolutionary biology courses for grouping behaviour. Starlings are preyed upon by hawks and falcons, and it is plausible to consider a murmuration as a continuous movement towards the safety of the centre. As a result, the centre never stabilises and the murmuration twists and turns in a perpetual escape motion.

There are several problems in viewing murmurations purely in terms of a selfish herd. Indeed, producing spectacular displays over the famous Brighton pier in Southern England every evening is probably not the best way to avoid the attention of predators. Instead, it could be that the murmuration itself provides a way of monitoring predators as they approach. Work in the 1970s showed that starlings in larger groups responded to the presence of a model hawk faster, and recent work has shown that the formation of 'waves' in murmurations is linked to reduced predation success by peregrine falcons. Waves propagate away from an attack, and so fluctuations in the local structure are likely also to be efficient in confusing potential predators.

Waves of turning away from attacking predators are a prime example of information transfer within animal groups. In this case, information about the predator propagates through the group, but in other examples of collective motion the information might pertain to food sources or roosting sites. Information transfer can therefore provide a general evolutionary explanation for the origin of many distinct forms of collective motion. However, to understand if this information transfer hypothesis can be linked to the structure and functioning of extremely large murmurations, we need to understand more about exactly how animals interact within these groups.

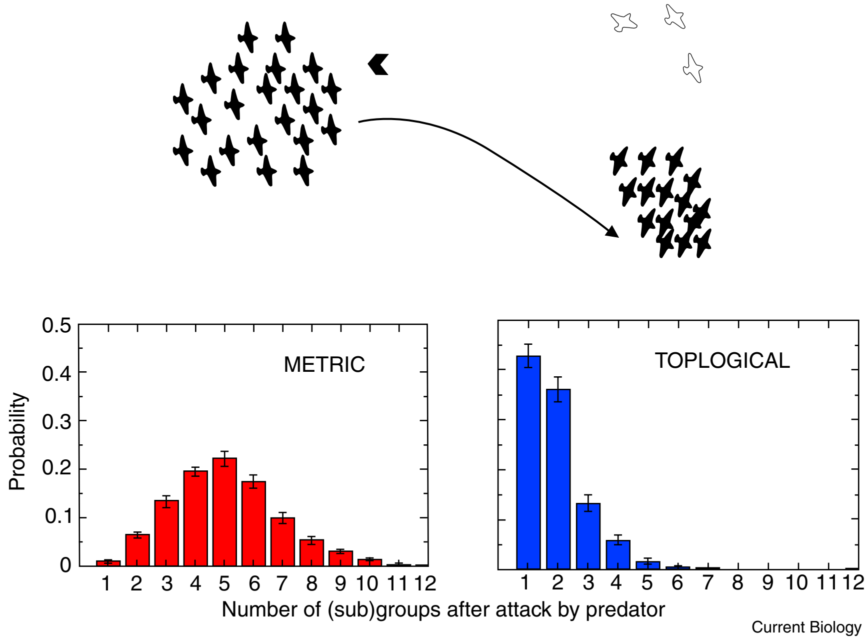

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Figure 2. Simulations of starlings (bird silhouettes) following metric- or topological-based interaction rules when under attack by a predator in relative motion to the flock (approaching arrow).
In the metric case, many birds are pushed out of the flock, resulting in fission and sub-grouping, whereas in the topological case, stragglers almost never arise. Figure redrawn from Ballerini *et al.* (2008).

How do murmurations occur? Today there is an excited and vibrant community of biologists, engineers, physicists and mathematicians all working together to understand collective motion. This research is interdisciplinary both because new techniques are needed to unravel the mysteries of collective motion and because, once revealed, these secrets could be used to design ‘intelligent swarms’ of robots. Numerous models of collective motion have been proposed, many of which display realistic-looking dynamics. However, these models usually rely on untested assumptions about what rules guide an individual’s movement.

Quite amazingly — given their apparent complexity — murmurations are among the first animal collectives for which empirical data are now available. The STARFLAG project is a European Commission-funded project that has conducted ground-breaking studies on the starlings of Rome. Using a series of interlinked cameras, they measured murmurations in three dimensions, reconstructing individual starling movements from the videos. STARFLAG researchers showed that starlings do not respond to their neighbours based on their metric distance — as most current models assume — but rather on the topological distance, where each bird appears to interact with a fixed number of neighbours that is, on average, six to seven birds.

Computer simulations have been used to link these findings back to the question of how murmurations might allow individuals to avoid predation. These simulations have shown that, when under attack by a predator, birds which use a topological rule that the researchers inferred from their video are not broken up by the attack. Such break ups are more probable in a model implementing metric rules (Figure 2).

Can we find the rules of interaction? There remain many questions about the in-flight interactions of the starlings. How many neighbours do starlings interact with? Do they try to take the same heading as their neighbours or are they simply attracted to them? Are interactions mediated through vision or perhaps by the dynamics of the airflow that the murmuration creates? Could the whole swirling pulsing murmuration be explained only in terms of avoiding collisions while keeping moving? Up to now, researchers have been observing from afar, using cameras, and building models that look like their observations. New bio-logging technology may allow us to get inside the murmuration. GPS and accelerometers can tell us not only where birds are positioned, but also how fast their wings are flapping. Researchers have already used this technology to show that pigeons have to work harder — flap their wings at a higher frequency — when they are in tighter kits. Data loggers can also record how a bird sees, hears, smells, and feels their immediate environment.

Even if we can collect detailed data of starling flights there remain technical challenges in how to use the data to answer questions about their interactions. Recent work on small groups of mosquito fish have established that they interact primarily with their single nearest neighbour, accelerating towards it if they are far away and decelerating if it gets too close. But the simplicity of these particular interactions is exactly the reason they can be quantified. If starlings interact with multiple neighbours, using a variety of sense data, then it becomes difficult to pick out exactly which are the key factors. Such interactions can make visualising interactions difficult and require new methods for model fitting and validation.

Why do we care about murmurations? While dissecting the details of interactions within murmurations is all very well, we also need to stand back and appreciate the bigger picture they represent. Collective motion produces just a few key dynamic shapes, or as some physicists say, universal patterns. Highly aligned groups, rotating mills and dynamic figure-of-eights are key examples. These types of patterns are observed not only in moving animal groups, but also in cell migration, bacteria populations, and even in many physical and chemical systems. The question is whether a few key mechanisms could explain similarities between these patterns. Identifying common features in different simulation models and in diverse biological systems may allow us to one day provide a direct link between interaction asymmetries and these universal patterns. That starlings and other birds characterise these universal patterns so well may explain our fascination with flocking. It could explain why during just two weeks in November, 5.3 million people watched Sophie Windsor Clive's Vimeo upload of her and her friend's sighting of a murmuration (http://vimeo.com/31158841). An evening murmuration is more than just the dance of starlings; it is a glimpse in to one of the fundamental motions of life.

Where can I find out more?

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Caveolae

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What are caveolae? Caveolae are invaginations of the plasma membrane with a defined omega (Ω) shape and a diameter of 60–80 nm (Figure 1). Caveolae, which can only be unambiguously identified by electron microscopy, were first noticed in 1953 by G.E. Palade and were described and named 'caveola intracellularis' by E. Yamada in 1955. However, it took almost 40 years to identify caveolins, the main proteins responsible for this unique plasma membrane domain. There are three mammalian caveolin genes: caveolin-1, caveolin-2 and caveolin-3. Smooth muscle expresses all three isoforms, while skeletal and cardiac muscle express only caveolin-3. Caveolins 1 and 2 are also expressed in non-muscle cells. Caveolae formation is strictly dependent on caveolin-1 or caveolin-3, depending on the tissue. Caveolin-2 appears to contribute to caveolae formation in some cell lines but is dispensable *in vivo*. Another family of proteins, the cavins (see below) have recently been shown to participate in caveolae formation. Caveolae are also found in complex structures harboring multiple caveolae that can form raceme- or rosette-like structures (Figure 1). Compared with the surrounding membrane, the membrane of caveolae is enriched in cholesterol and certain sphingolipids.

Not to be confused with... Lipid rafts. A consensus definition of lipid rafts was agreed at a Keystone meeting in 2006: "membrane rafts are small (10–200 nm), heterogeneous, highly dynamic, sterol- and sphingolipid-enriched domains that compartmentalize cellular processes. Small rafts can sometimes be stabilized to form larger platforms through protein–protein and protein–lipid interactions." Based on this widely-accepted definition, membrane rafts and caveolae denote distinct membrane domains. Contrary to lipid rafts, caveolae are quite homogeneous in size and have a defined curvature. In addition, caveolae are normally quite static. However, lipid rafts and caveolae do have some features in common, such as their enrichment in cholesterol and certain sphingolipids.

Are caveolae present in all cells and organisms? Caveolae have been identified in several mammals and in zebrafish, but not in *Caenorhabditis elegans*, despite the presence of caveolins in this organism. Honeybee caveolin is able to form caveolae but surprisingly no caveolin gene has been identified in the fruit fly. Caveolins are restricted to metazoans, and are absent from fungi, plants and non-metazoan parasites. In humans, caveolae are abundant in endothelial cells, adipocytes, smooth muscle cells and fibroblasts but are absent from red blood cells, platelets and lymphocytes. The fact that mice lacking caveolin-1, 2 or 3 are viable but show phenotypes in multiple tissues strongly suggests that caveolae represent an advantage for certain cells, but that life can go on without caveolae.

What regulates caveolae formation? Cholesterol plays a major role in caveolae formation, as its depletion flattens caveolae. Caveolae are also flattened by physical stretching of cells or inflation by placing cells in hyposmotic medium, suggesting a role in mechanosensing and mechanotransduction. Caveolae have only been observed at the plasma membrane and there is no evidence for their formation in endomembranes, despite the presence of multi-oligomerized caveolin-1 complexes in the Golgi. Therefore, specific factors needed for caveolae formation must be present or active only at the plasma membrane. A second family of proteins, the cavins (a family of four proteins), has recently been shown to be important in caveolae formation. Reduction in the levels of cavin-1 (also known as PTRF), cavin-2 (SDPR) or cavin-3 (SRBC) correlates with reduced caveolae density. Cavin-4 (MURC) is expressed predominantly in muscle and is probably a caveolae component, but its role is unclear. Although few studies have examined the role of cavins, direct or indirect interaction between cavins and caveolins appears to be important for caveolae formation, stability and possibly trafficking. However, more studies are needed to define the role of each cavin. It is very possible that other, as yet unidentified factors are needed for caveolae formation. A recently identified candidate is the membrane curvature regulator pacsin2, which has been implicated in sculpting caveolae.