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Safety in numbers

William Foster discusses the classic 1981 Nature paper 'Evidence for the dilution effect in the selfish herd from fish predation on a marine insect' that he published with John Treherne.

The radio reporter switched on her tape-recorder and, looking up encouragingly at the white-haired scientist sitting next to me, said: 'So, tell me, John Treherne, why do animals live in groups?' John paused to consider a suitably enlightening response. A complicated series of possibilities seemed to be passing through his mind and after a slow rasping intake of breath, which I thought might go on forever, he said: 'I dunno, really.' We had to regroup. The best answer we could think of was: 'Because there is safety in numbers'.

This interview was taking place in October 1981, in the Zoology Department at the University of Cambridge, UK, triggered by a paper that John Treherne and I had just published in Nature (Foster and Treherne, 1981). At that time, John had been the Editor in Chief of the Journal of Experimental Biology since 1974, and would continue in that role until his death in 1989: I was one of the two Assistant Editors, from 1975 to 1998. The paper provided the first quantitative field evidence of the way that animals might gain protection from predation by seeking cover in a group of other similar animals. This protection is known as the dilution effect. An animal on its own is clearly at high risk if a predator notices it, but if it is in a group of N animals, it now has only a $1/N$ chance of being eaten. According to this idea, an animal joins a group with the selfish expectation that someone else will become the victim.

This straightforward notion had already been discussed by George Williams (Williams, 1966) and Bill Hamilton (Hamilton, 1971), who developed the idea of the dilution effect as a pivotal example of how explanations for animal behaviour could be sought most profitably at the level of individuals behaving selfishly rather than cooperatively to ensure the survival of the population or species. Hamilton discussed the idea most fully in a truly copper-bottomed classic paper entitled 'Geometry for the selfish herd' (Hamilton, 1971), which opens with the memorable sentence, 'Imagine a circular lily pond'. In his scenario, there is a one-dimensional line of frogs arranged on the perimeter of the pond, disconsolately contemplating the appearance of a snake that will emerge and eat the nearest frog. In a desperate attempt NOT to be the nearest to the snake, each frog will move closer to other frogs, thereby reducing its domain of danger: a frog group would automatically arise from the single cause of each frog selfishly taking cover behind other frogs.

By the late 1970s, these ideas of individual-based selective advantage had reasonably wide traction amongst scientists who were beginning to describe themselves as behavioural ecologists. But this was a young field and there was a shortage of good quantitative field evidence to put flesh on the ideas of Hamilton and other pioneering evolutionary biologists. The chief problem in studying group-living in any specific context is that there will almost always be a range of conflicting adaptive explanations: group-living might enhance feeding or mating, and it might reduce predation by providing improved detection or confusion of the predator, as well as by dilution effects. This makes John Treherne's unwillingness to provide a snappy answer to the interviewer's question a good deal more understandable. It also accounts for the simplicity of Hamilton's lily-pond scenario: the frogs are not eating or mating, and the snake's approach is unseen and cannot trigger early avoidance or confusion behaviour.

The animals that John and I had been studying provided a remarkably close real-life version of Hamilton's lily-pond frogs. We had been looking at the marine insect *Halobates robustus* (Hemiptera: Gerridae), which lives on the surface of the sea in sheltered coastal areas of the Galapagos Islands (Beebe, 1924). It was in fact insect natural history, not behavioural ecology, that had sparked our interest in these marine water striders. The genus *Halobates* is of enduring fascination to entomologists, as it contains the only species, out of an estimated 3.7 million (Hamilton et al., 2010), that have successfully colonized the open seas (Andersen and Cheng, 2004). In 1978, John Treherne had been invited to take part in a research programme of a Scripps Institution of Oceanography expedition to the Galapagos Islands, so that he could apply his expertise in neurophysiology in an attempt to understand why only insects of this particular genus had been able to overcome the physiological challenges of life at sea. He quickly realized that the top priority was not to indulge in sophisticated neurophysiology but to watch, and perhaps film, the insects and find out what the individuals were actually doing.

We noticed that the insects lived in groups, which we called flotillas, of different sizes (from one to over a hundred) and realized that this grouping behaviour was probably the insect's only mode of defence against predation. During our second visit to study these insects, we stumbled across a predator – a juvenile sardine – which swims some way below the surface and hunts the insects by swimming up swiftly to the surface, pecking briefly at an insect, and then rapidly swimming down back to re-join the fish school. Like the snake, the fish is not visible to its prey as it approaches from under the water: group size cannot therefore enhance predator detection or avoidance behaviour. The insects we were observing were not feeding or mating. And like the frogs, the ocean striders are confined, albeit in two dimensions rather than one: they cannot fly or dive below the water but must stay on the surface of the

Classics is an occasional column, featuring historic publications from the literature. These articles, written by modern experts in the field, discuss each classic paper's impact on the field of biology and their own work.

waves. The stage was set, although I do not think that either of us fully realized this at the time, for a quantitative test of the importance of the dilution effect.

Although the insects are only a few millimetres long, they were relatively easy to observe on the mirror-calm surface of the sea. We settled down on the unforgiving black lava and kept watch, through our binoculars, on flotillas of different sizes, including solitary individuals, for periods of five minutes and counted the number of attacks on them. We found that the attack rate by the fish was similar for groups of different sizes, clearly demonstrating that the attack rate per individual varies simply on the basis of the dilution effect. An insect in a group of 100 is about 100 times less likely to be attacked than an insect on its own. In the figure that we published in the Nature paper, the predicted line is the result that would be produced if the decline in attack rate per individual depended entirely on the dilution effect: the observed line is not significantly different from it (Foster and Treherne, 1981; Treherne and Foster, 1982). This clear, readily understandable, demonstration of the dilution effect, which was based on simple observations made over a few hours on two afternoons, made its way into the early textbooks of behavioural ecology, notably *An Introduction to Behavioural Ecology* (Krebs and Davies, 1981), and still survives in several of them.

In addition to these observations on the defences provided by group-living to unseen predators, we also studied how these ocean striders might defend themselves from predators whose approach they could detect. We were able to investigate several distinct advantages that they gain from group-living, including early detection and confusion of the predator, and information transfer within the group. We demonstrated that larger groups were able to respond to the approach of a detectable predator sooner: the predators we observed were a yellow warbler, *Dendroica petechial*, and a surface-feeding mullet, but in our experiments we used a revolving white Perspex rectangle (our field notebook) on a string (Treherne and Foster, 1980). This was one of the earliest and most data-rich examples of how group-living might enhance predator detection.

We also became interested in how information about an approaching predator might spread through a group of ocean skaters. To do this, we filmed eight different flotillas and, using frame-by-frame analysis, measured the track and velocity of each individual and its position in the flotilla as the model predator approached from one side. From this, we could easily compute the speed with which the wave of excitation, as the insects bumped into each other, spread across the flotilla. This turned about to be about 60 cm s^{-1}, which greatly exceeds the rate of approach of the model predator (about 8 m s^{-1}). We called this wave of information the ‘Trafalgar effect’ because it reminded us of the series of signals that were transmitted along a chain of ships to HMS *Victory* before the Battle of Trafalgar, which told Nelson that the combined French and Spanish Fleet was leaving Cadiz, even though it was way beyond the horizon of his flagship (Treherne and Foster, 1981).

Our research did not lead to an explosion of further detailed research on anti-predator behaviour in *Halobates*, apart from some confirmatory research by us on other species (Foster and Treherne, 1986). I think this was because the ocean striders, although an excellent model system in many respects, cannot be kept for any length of time under experimental laboratory conditions (e.g. Herring, 1961). They are accustomed to the utter cleanliness of the surface of the always self-renewing sea and a few motes of dust or films of grease on laboratory seawater kills them off.

The dilution effect paper was useful in providing evidence for an important idea of widespread applicability. The concepts associated with the idea of the dilution effect have become more sophisticated since 1981, in particular the fact that detectability cannot be divorced from attack risk, an issue which our observations rather skated over. The most compelling evidence for the dilution effect in the selfish herd comes from field experiments by Alta De Vos and Justin O’Rian, who studied Cape fur seals, *Arctocephalus pusillus*, being attacked by great white sharks, *Carcharodon carcharias* (De Vos and O’Rian, 2010). They directly varied the distance between individual decoy seals in groups of four or five, and recorded how often the individuals were attacked by sharks as a group of decoys was towed behind a boat. They were able to confirm the central concept of the selfish herd hypothesis: the size of an individual’s domain of danger is proportional to its predation risk. The bigger the domain the bigger the risk.

The Trafalgar effect paper (Treherne and Foster, 1981) is perhaps the most conceptually important of our studies on group behaviour in *Halobates*. It was one of the very first papers to demonstrate the idea of behavioural contagion – the importance of the social transmission of behaviour within animal groups (Krause and Ruxton, 2002; Rosenthal et al., 2015). It is now possible to analyse the movements of individual animals within complex three-dimensional groups (e.g. Handegard et al., 2012; Strandburg-Peshkin et al., 2013; Rosenthal et al., 2015). A key feature of these studies seems to be that major elaborate changes in group behaviour can emerge just from small changes in the responses of individuals to their neighbours, following fairly simple rules (e.g. Couzin et al., 2002). This realization is especially welcome for anyone raised amongst the nuanced thickets of ethology, whose practitioners often seemed to relish the idea that complex behaviour always requires a complex explanation.

This period when we were travelling to the Galapagos in 1979 and 1980 marked the start of my career as an independent scientist. From John, who was basically a bench scientist, I learned how to extract quantitative information from what looked like an intractably messy field environment; how to improvise and make useful observations with very basic equipment; and how to remain flexible and nimble in the face of a rapidly changing research agenda. Above all, I learned that doing research ought somehow to be fun.

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