The sum of the parts

Birds do it, bees do it and collective nouns like flocks and herds, swarms and shoals describe it. **Lesley Morrell** weighs up the risks and benefits of the herding instinct.

Many animals actively seek out the company of others. While we understand how animals choose between established groups – an individual might prefer to join a larger group over a smaller one, or a group where the members are of a similar size to the chooser – we know surprisingly little about how groups form in the first place.

Think of the way huge flocks of birds or schools of fish all move together. Each individual in the group cannot possibly know what all the others are doing, so how is it that these groups seem so organised? My fellowship work aims to understand these mechanisms, using both computer models and experiments with small fish. By using self-organisation principles (where each individual in the group responds to those around it by moving away from or towards them, or aligning themselves in the same direction), biologists have been able to shed some light on the herding instinct. If each animal pays attention to only some of its nearest neighbours, then we can easily recreate patterns in computer models like the ones we see in nature. What we don't yet know is how many others each individual pays attention to, or the strength of these influences.

When animals are frightened, perhaps because they detect a predator, escape becomes their overriding motivation. Under these conditions, many animals group more tightly together. In 1971, the British evolutionary biologist William Donald Hamilton proposed the selfish herd theory. He asked us to imagine a circular lily pond, around which lives a colony of frogs, and in which lives a predatory water snake. When the snake gets hungry, it surfaces somewhere near the edge of the pond, and attacks the nearest frog. Each frog is surrounded by an area which is closer to it than to any other frog, and if the snake appears in the area, it attacks that frog. Hamilton called this area the 'Domain of Danger', and proposed that to minimise its risk of being eaten, each frog should try to minimise its domain of danger. An individual frog could do this by jumping into the space between its nearest neighbour and its neighbour's neighbour.

Consider next a herd of gazelles, grazing on the plains of Africa. Hiding in the grass is a lion. The gazelles know that the lion is there, perhaps because they hear it roar, but they don't know the direction of attack. How does each gazelle reduce its domain of danger? Hamilton also considered this, and suggested that a simple 'movement rule' that it could follow would be to move towards its nearest neighbour. He used mathematical modelling to show that if all the gazelles followed this rule, then they would group together, but into small groups and pairs, rather than into the large groups that we see in the wild.

To deal with this problem, scientists have devised increasingly complex movement rules, such as taking into account the position of multiple neighbours, or weighting the effect of a neighbour by its proximity (so that closer neighbours have greater influence on an animals preferred movement direction). Using mathematical models, they have found that the more complex the rule, the tighter the shoaling or herding, making the rule more 'successful'.

But we were interested in the effects of ecological factors on the success of different movement rules. Do the complex rules still perform well when we investigate the size or the density of a group, or the time at which the predator attacks?

We found that these ecological factors do have important effects. Using mathematical models, we tracked the movement of artificial animals as they were stalked by artificial predators in two dimensions, calculating the size of their domain of danger over the course of ten seconds of movement. We found that we don't need to discard simple rules (where individuals only take account of their nearest neighbour) in favour of more complex ones (where multiple neighbours are taken into account), when we consider ecological factors.

On the contrary, we find that the simplest rules are more effective at reducing the probability that a predator will detect a group in three situations: where animals are quite widely spaced; when groups are large; and when predators attack quickly after the animals begin moving to escape. Simple rules work well in these situations because they allow animals to form small groups quickly, while following a complex rule means the animal is moving alone and more vulnerable to attack. The complex rules are best when groups are already compact, when groups are small, and when there is ample time for the prey to move before the predator pounces. Only the complex rules produce large, compact aggregations, but these form more slowly than the smaller groups produced by simple rules, suggesting that there may sometimes be a trade off between the safety of the group and the time it takes to get there.

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Although the models produce useful predictions, which may help with our understanding of collective behaviour of animals, what we need now are studies of real animals pulling together when startled by a predator, so that we can work out what is going on in natural populations. ❖

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