documented gene transfer to the host nucleus, and import of proteins back to the endosymbiont. Such profound functional and genetic interconnectedness raises the question of whether such partnerships represent two distinct organisms or a unified amalgamation.

While some endosymbiotic interactions have been known for many years, it is humbling to remember that numerous associations were completely unknown just a few decades ago, or even a few years ago. Even among the long-studied associations, our understanding of underlying mechanisms is expanding thanks to new approaches to study the physiological and genomic basis of these relationships. Endosymbiosis remains rich with mysteries, but one thing we know for sure is that our current understanding is just the tip of the iceberg. Future work promises to shed light on the mechanisms by which endosymbioses are established and maintained, and to reveal a diversity of previously unknown interactions that shape ecosystems ranging from the deep ocean to our own back yards.

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Selfish-herd behaviour of sheep under threat

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Flocking is a striking example of collective behaviour that is found in insect swarms, fish schools and mammal herds [1]. A major factor in the evolution of flocking behaviour is thought to be predation, whereby larger and/or more cohesive groups are better at detecting predators (as, for example, in the 'many eyes theory'), and diluting the effects of predators (as in the 'selfish-herd theory') than are individuals in smaller and/or dispersed groups [2]. The former theory assumes that information (passively or actively transferred) can be disseminated more effectively in larger/cohesive groups, while the latter assumes that there are spatial benefits to individuals in a large group, since individuals can alter their spatial position relative to their group-mates and any potential predator, thus reducing their predation risk [3]. We used global positioning system (GPS) data to characterise the response of a group of 'prey' animals (a flock of sheep) to an approaching 'predator' (a herding dog). Analyses of relative sheep movement trajectories showed that sheep exhibit a strong attraction towards the centre of the flock under threat, a pattern that we could re-create using a simple model. These results support the long-standing assertion that individuals can respond to potential danger by moving towards the centre of a fleeing group [2].

Upon detecting a potential predator, animal aggregations are often said to 'close-in' on themselves [3]. However, attempts to quantify individual animal spacing and relating this to risk are impeded by the inherently unpredictable nature of predator attacks. Thus, our understanding of this selfish herd behaviour has largely been informed by computer simulations and modelling [1–4], and actual positional changes of individuals during an attack has only been studied in a few cases [5,6]. In 1973, Hamilton [3] cited sheep flocking behaviour in response to a herding dog as an anecdote in support of his selfish-herd theory. We have quantified sheep flocking in response to herding by a dog in a controlled but naturalistic setting. In our experiments, a trained Australian Kelpie working dog was directed verbally to herd a flock of initially resting sheep (n = 46 individuals) to a target zone (an open gate) with minimal guidance (given the command "bring them home"). Both the sheep and the sheepdog were fitted with a 'data-logger' [7,8] on a harness (Figure 1C) that comprised a GPS module and antenna, a microcontroller, data storage card and a rechargeable battery (see Supplemental Experimental Procedures for details).

We collected data during three herding events, and re-constructed the position of all sheep in Euclidean space every second from our GPS data (see Supplemental Movies S1–S3). From this positional information, we calculated the flock's geometric centre — the centroid — and the dog's distance to this flock centroid on a second-by-second basis. Then, since sheep are predicted to move towards the centre of the flock under attack [3], we calculated the distance of all sheep to the flock centroid each second. The mean of all sheep distances to the flock centroid represented a measure of 'flock cohesion'. These data were explored, providing the first quantification of sheep flocking response to a herding dog (Figure 1).

Inter-sheep distance and overall flock configuration varied at the start of each of our trials. In each trial the flock responded to the approaching dog (began to move) at a distance of around 70 m (Figure 1A), and demonstrated classic aggregation and avoidance behaviour (Figure 1A; Supplemental Movies S1–S3). Individual sheep moved towards the flock centroid until they were in a tight cluster [3], with sheep farthest from the centroid moving the greatest distance (Figure 1B). The time taken for this transition from a dispersed to a clustered state to occur was proportional to initial flock cohesion (Figure 1A), suggesting that the sheep moved towards the flock centre at a

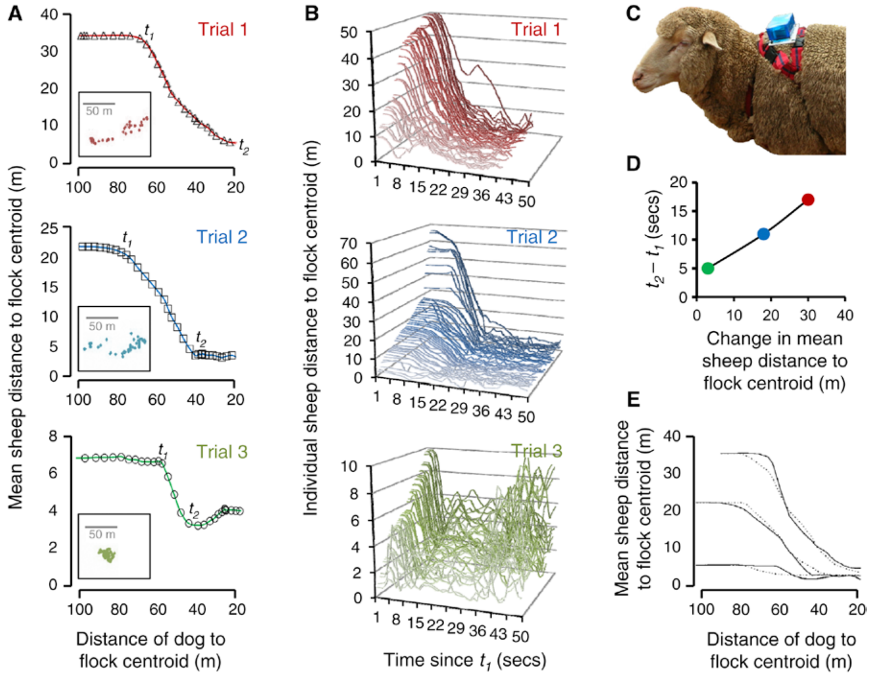

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Figure 1. Flocking response of sheep to a herding dog.

(A) Flock cohesion, measured as the mean distance of all sheep from the flock centroid (m) as a function of dog-distance (m) from flock centroid, for three herding trials. The flock configuration prior to the approach of the dog, i.e. where the flock is stationary and dispersed, is indicated by time t_1, and is shown as an inset for each trial. t_2 indicates the time the flock cohesion stopped declining, i.e. although sheep position changes, all sheep were packed side-to-side. Note that the scale is different for trials to better illustrate the transition. In each trial the flock cohesion stabilises at ~4 m after an initial collapsing (which is visible in trial 3 due to the scale used). (B) Plots of individual sheep ($N = 46$) movements relative to the flock centroid as a function of time since t_1. Sheep are ordered by initial distance from flock centroid. (C) A sheep wearing a data-logger. (D) Change in mean sheep distance to flock centroid (m), as a function of time taken (secs) for the flock to coalesce to a clustered state (i.e. the difference in flock cohesion at t_1 and t_2). (E) Experimental data (lines) and data generated by a simple model (dotted lines). See Supplementary Information for further details.

similar speed across our three trials (Figure 1D). With this information, we were able to fit a model to this transition using a first order differential equation (Figure 1E; Supplemental Information). We assumed $N = 46$ sheep to be distributed across a field with flock cohesion equivalent to those seen in each of our three individual trials, and that the sheep showed a strong attraction to the flock centroid when the dog approached within a certain radius of the flock centroid.

This model performed well, producing a flock response that was qualitatively similar to that seen in our experiments (Figure 1E), and it actually performed better than a model in which sheep showed attraction towards the flock centroid when the dog came within some distance of the nearest sheep (see Supplemental Information for further details of the model). Together, our experiments and the model suggest that the sheep appear to be considering the position of multiple neighbours in order to move towards the centroid [1,2]; a precise calculation of the flock centroid may be unlikely, but sheep may be able to approximate where that target location ought to be.

Whether the patterns we have revealed are observed in flocks of different size, activity states, and threat type remains to be seen. However, it is clear that the ability for researchers to track individual movements relative to one another will be important in evaluating potential mechanisms underlying the selfish herd behaviour we have described [8,9]. Reverse engineering the specific local interaction rules that the sheep are using is the logical next step [1], and is something we are now actively researching. Our approach could also be used to understand breakdown of group behaviours that may result from abnormalities in individuals (such as injury or illness), or from diseases that affect multiple animals. For instance, slowly progressing neurological disorders that include cognitive and social behavioural abnormalities such as scrapie or the transgenic sheep model of Huntington's disease recently reported could be detected and tracked over time [10].

Supplemental Information

Supplemental Information includes three movies and supplemental experimental procedures and results and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.05.008.

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