How social skills are shaped in an ever-changing world

Seirian Sumner

Collective behaviours are prominent throughout nature — from groups of genes being activated in tandem, to shoals of fish swimming together for protection from predators, to mounds of insects working to build nests. But biologist Deborah Gordon worries that the researchers who study how these phenomena evolved are missing a trick. In *The Ecology of Collective Behaviour*, she argues that evolutionary biologists often fail to consider that the ever-changing environments in which animals live are fundamental to shaping collective behaviours. She aims to set the record straight.

Gordon has devoted decades to studying the natural history of two species of ants that live in very different environments, paying acute attention to how their stirring, dynamic habitats shape their behaviour. These observations form the bedrock of her book.

First up is the red harvester ant *Pogononyrmex barbatus,* which lives in the harsh, parched deserts of New Mexico. Affectionately known as Pogos, these ants are deep red and around 7 millimetres long — impressive for an ant. They live in colonies of more than 10,000 female workers (who do all the work in ant, bee and wasp colonies), using seeds scattered on the desert floor for both food and water. Seed sources change through the year as different plants wax and wane. These shifts are slow and predictable, and there is mostly a plentiful and constant supply of food. But collecting seeds is hazardous: deserts are dry, so Pogos live in a catch-22 world: they must risk desiccation to gather the water they need.

Gordon shows that this delicate trade-off is achieved by a slow but robust mechanism through which foragers recruit nestmates to search for food. When a female returns to the nest with her bounty, hydrocarbons laced across her cuticle are released, indicating to her sisters that there’s food out in the desert.

Just a flighting touch of a forager’s antennae sends others scuttling from the nest. They head out in random directions, but that’s OK, because seeds are spread across the desert floor, not clustered in patches. Plentiful food and favorable environmental conditions — days that are not too hot, for instance — mean many foragers returning to the colony, recruiting many new foragers. Conversely, bleaker conditions mean fewer ants return to muster new recruits. In this way, simple positive feedback regulates the steady collective behaviour of thousands of ants.

Next Gordon turns to the arboreal turtle ant, *Cephalotes goniodontus*, which forages in the canopies of the dry tropical forests of Mexico. Unlike the desert harvesters, turtle ants spread their brood across many nests perched in the canopy, connected by a complex net of ever-tangling vines, shifting leaves and moving stems. Their food sources are ephemeral — foragers must exploit bursts of nectar in transient floral blooms.

Each foraging turtle ant lays a trail of pheromones wherever she goes — whether she’s discovered a food source or not — whilst following the trails laid by others. These trails constantly bifurcate, and can change on an hourly basis. Which route should each forager follow?

The answer is simple, Gordon reveals: the ants follow the smelliest path — the one with the strongest pheromone signal — and keep laying and reinforcing profitable trails until something tells them to stop, be it a predator or congestion at the nest. This ensures that the ants can find the current most lucrative forage patch, and can adjust information flow rapidly, changing behaviour with their ever-changing environment.

Pogo and turtle ants solve similar problems in very different ways. How they do it is dictated by their environment. Gordon borrows concepts from network science to describe how turtle ants function in modules — units within which most information flow occurs — to keep information flow local, enabling them to respond rapidly to ever-changing resources. By contrast, the centralized regulation of Pogo ants is the epitome of low modularity, with the nest the sole source of communication.

Gordon argues that the nature of the environment and the resources it provides determine the type of collective foraging mechanisms that evolve — not just for ants, but for all social life. The extent to which ecology drives the evolution of social behaviour in this way has been overlooked, she claims.

I agree that researchers need to better recognize that organisms exist, and have evolved, within the dynamic, often unpredictably messy world of ecology, and to acknowledge that this does influence their behaviour. I admire how the author takes inspiration not just from careful field experiments — removing ants or changing resources and observing how they respond — but also from the old science of natural history. Many evolutionary biologists could learn a lot by rediscovering this way of working.

But I am less convinced by Gordon's claim that her ideas are at odds with the 'prevailing theory' for social behaviour. 'Inclusive fitness theory'[2] — an idea put forward by evolutionary biologist William D. Hamilton in 1964, and widely accepted in the field — posits that social behaviours evolve when the benefits of cooperating exceed the costs (Hamilton, W. D. *I. J. Theor. Biol.* **7**, 1– 16; 1964). Hamilton's ideas stemmed from his observations of wasps, ants, bees and birds in their natural habitats, and are supported by strong experimental and theoretical evidence. For instance, when breeding is risky for clownfish, perhaps because there are lots of predators close by, some fish stay at home and help raise others' young (Branconi, R. *et al. Commun. Biol.* **3**, 1–7; 2020).

The confusion arises because, I feel, Gordon conflates proximate (mechanistic) and ultimate (evolutionary) processes. Her book offers useful insights into proximate processes by which collective behaviour is regulated day-to-day, and the role of the environment in shaping and maintaining these; and I agree that these are increasingly overlooked as we've become more divorced from studying organisms in their natural environments. But these insights are not at odds with the prevailing theory for how collective behaviour evolves.

In closing, Gordon returns to the ants, remarking: "The whole appears to be more than the sum of the parts, because the parts do not sum – they intertwine, jostle and respond". This heartening statement is a great description of the messy world of ecology and evolution. It's a truth that all biologists should keep in mind.

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