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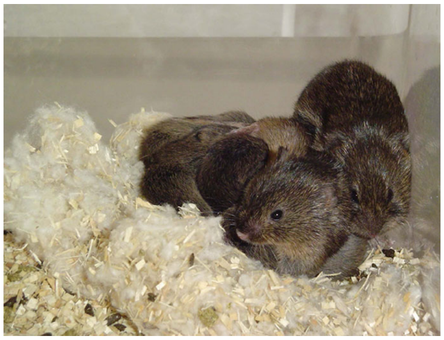
Social evolution: from molecules and superorganisms to flocks, shoals and parenting



Social prairie voles. Photo credit: Karen Bales.

No matter how small or large, from bacteria and amoebae to the planet's largest mammals, all organisms interact socially with other members of their species. Social organisation – whether conspiring to construct vast colonies, shoaling for comfort or uniting to raise offspring, provides the infrastructure for life. However, social behaviours also have implications at the genetic level. Gene pathways can influence group dynamics and how individuals behave socially can affect the ability for genes to be passed on – it is these phenomena that fascinate Joel Levine from the University of Toronto, Canada, and Daniel Kronauer from the Rockefeller University, USA.

According to Kronauer, there are many examples of social behaviours that are beneficial at the genetic level, although these behaviours may not be beneficial from the perspective of the individual. 'You can have cases where natural selection acts to promote the [evolutionary] fitness of a genetic element [gene] at a significant cost to the fitness of the individual', explains Kronauer, giving the example of ant colonies, where sterile workers that are unable to pass on their genes perform essential social functions as part of the colony. 'They have zero "fitness"', says Kronauer. However, he explains that the workers' behaviour still allows their genes to be passed on by queen ants. Even though the individuals do not benefit directly from their social behaviour, the colony benefits from transmission of genes that are fundamental to the colony's survival.

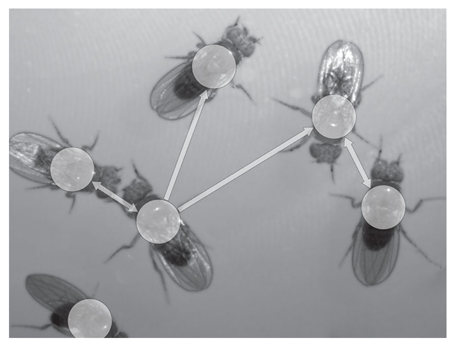
Together, Levine and Kronauer have guest edited a series of review articles for Journal of Experimental Biology that are dedicated to our growing understanding of the evolution of social behaviour; how individuals interact, how these interactions have produced the social structures that we see today and how they may evolve further. Published together, the reviews discuss the evolution of social behaviour in species ranging from microbes, ants and termites to amphibians, rodents and birds. They also explore the radiation of social constructs from genomic evolution to the sophisticated social interactions that can emerge from relatively simple individual interactions throughout all taxa.

Molecular and microbial social behaviour

Reducing existence down to the fundamental genetic components that underpin life, Richard McLaughlin Jr and Harmit Malik from the Fred Hutchinson Cancer Research Center, USA, discuss the propagation of 'selfishness' at the molecular level (pp. 6-17). Explaining that individual selfishness conflicts fundamentally with the benefits of communal living, McLaughlin and Malik then describe how selfish genetic factors ensure their propagation through one of two possible mechanisms: over-replication or elimination of competitors. In the first scenario, selfish genetic elements, such as transposons or infectious viruses, ensure their propagation in host cells by mutating rapidly to out-fox the body's defence mechanisms. In the second, some selfish genetic elements ensure their propagation by eradication of cells that do not carry the selfish gene. The duo says, 'This diversity attests to the fact that genes and genomes have been remarkably opportunistic and inventive to exploit every possible advantage in the Darwinian struggle for survival'.

On the microbe scale, many single-celled organisms have evolved a wide range of social behaviours that allow them to interact cooperatively, from predatory *Myxococcus xanthus* bacteria, which swarm to hunt, to the cellular slime mould *Dictyostelium discoideum*, in which individual cells assemble to form a slug before producing a fruiting body that releases spores to reinitiate the life cycle. Outlining the benefits of cooperation for microbes and the factors that prevent these forms of social behaviour from being undermined by cheaters, Corina Tarnita from Princeton University, USA, discusses how studying microbial communities can teach us about the evolution and maintenance of cooperative social behaviours (pp. 18-24). However, she warns that our poor understanding of the ecology of most microbial communities may result in misinterpretation of some microbial social behaviours if key ecological factors are neglected, and adds that anthropomorphising the concept of cooperation – such that examples of beneficial cheating are overlooked – presents another challenge.

Tracking and *Drosophila* social behaviour



Tracking *Drosophila* social interactions. Photo credit, Jonathan Schneider.

Monitoring the behaviour of individual organisms requires determination and painstaking attention to detail. Although manual tracking of multiple creatures is unachievable, even for modest social structures, Roian Egnor and Kristin Branson from the Howard Hughes Medical Institute, USA, explain that recent research into social behaviour has benefited enormously from advances in automated measurement and quantification of social interactions (pp. 25-34). Approaching the challenges inherent in the automation of tracking large groups of individuals, Egnor and Branson with

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colleagues Alice Robie and Kelly Seagraves summarise the factors that are essential for successful automation and meaningful interpretation of the results – including good lighting when filming, ensuring a clear view of all protagonists, the provision of a rich environment to encourage natural behaviours and reliable identification procedures. Applying their tracking algorithms, Branson's team can automatically extract posture information and location at each moment, before using pattern recognition algorithms to identify specific behavioural patterns that they then test to determine whether the behaviour is truly social. Listing examples in vertebrates and invertebrates where automated tracking procedures have identified behaviours that would have been overlooked previously, Branson and colleagues say, 'Advances in hardware, software and algorithms have made automated analyses of social interactions increasingly powerful and available'.

Following Branson's review of automated behaviour tracking, Pavan Ramdya from the California Institute of Technology, USA, in partnership with Jonathan Schneider and Joel Levine from University of Toronto at Mississauga, Canada, discuss how these sophisticated computational tools are being used in association with powerful genetic techniques to uncover the molecular and neuronal architecture that underpins communal behaviour in social *Drosophila* (pp. 35-41). The authors first review Schneider and Levine's recent study that showed how sensory genes are essential in the formation of *Drosophila* social networks, before discussing Ramdya and colleagues' investigation of the impact of group density on odour avoidance by the fruit fly. In the review, Ramdya and colleagues describe how they were surprised to find that, 'Individual odour avoidance increased when animals were placed in groups of densities similar to those found on a food source'. They then explain how they used a combination of computational and genetic techniques to identify a unique touch sensory gene that is responsible for the flies' collective avoidance of repellent odours, in much the same way that physical contact drives human stampedes.

Levine and Schneider then contribute to a second review, in collaboration with Jacob Jezovit from the University of Toronto, in which they compare the impact of light on mating behaviour and the hydrocarbon pheromones of 70 species of *Drosophila* with the ecological constraints under which they have evolved – arid species versus temperate and tropical specialists, and generalists with a global distribution (pp. 42-52). Focusing on the 47 species for which mating behaviour is available, Jezovit and colleagues investigate how similar habitats and environmental pressures may shape social behaviours including mating. Comparing the length of the hydrocarbon pheromone molecules on the fly abdomen, the trio found that the hydrocarbon profiles reflected the flies' environment reasonably precisely, with the arid species producing the longest hydrocarbon chains. They say, 'Based on the lack of visual communication that has been observed in arid species from field studies, perhaps non-visual communication is more efficient since arid *Drosophila* may rely on temperature-defined timing in activity in order to escape the extreme conditions'.

Superorganism social evolution

King and queen termites. Photo credit, Kenji Matsuura.

Within complex social insect societies, every inhabitant has a specific caste, or role, from reproductive queens to workers that provide defence, ensure the food supply and nurture the next generation. Together, these individuals function instinctively and integrate seamlessly within their community to produce a vast entity that behaves like an individual organism: a superorganism. How these highly coordinated social structures develop and evolve intrigues Waring Trible, Kronauer and Kenji Matsuura.

In their review, focused on the development and evolution of caste systems in ants, Trible and Kronauer define castes as individuals that share characteristics and explain that adult size is the main determinate of an ant's caste within the colony (pp. 53-62). In addition, the characteristics associated with individual castes switch from worker-like characteristics in the smaller ants to queen-like characteristics in the largest ants. As adult size is so tightly correlated with ant caste and role within the colony, the factors that regulate body size, such as the hormones ecdysone and juvenile hormone, temperature and nutrition, also regulate caste development. Moving on to consider how different caste structures have evolved through the loss and gain of caste strata over time, Trible and Kronauer review the literature which suggests that caste evolution occurs via modifications to the size distribution within the colony and the mechanisms that couple caste-characteristic development to adult body size.

Focusing on another group of social insects, termites, Matsuura from Kyoto University, Japan, discusses how some of these species have evolved a novel reproductive scheme – asexual queen succession – where the queens control the ability of sperm to fertilize eggs in order to take advantage of both sexual and asexual reproduction (pp. 63-72). This allows the queen to produce queen successors asexually – by producing replacement clone-queens to ensure the perpetual continuation of her genes throughout the life of the colony. She can also reproduce sexually with king termites to maintain genetic diversity. In this way she can produce workers and soldiers to work within the colony, as well as females that leave to establish colonies of their own. The queen's use of both asexual and sexual reproduction allows her to take advantage of the benefits offered by both reproductive systems, to maximise her contribution to the gene pool through asexual reproduction, while maximising diversity in the colony through sexual reproduction.

Ants in action

Cooperative ants transporting a CD. Photo credit, Dr Ehud Fonio.

Harnessing the power of the individual for the benefit of the collective is central to the organisation of all superorganisms, and individual social insects accomplish this without the benefit of oversight. Ofer Feinerman from the Weizmann Institute of Science, Israel, and Amos Korman from the University of Paris Diderot, France, (pp. 73-82) review how social insects

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employ an arsenal of communication tactics to convey information between individual nest mates – from pheromone scents and physical contact to visual signals and vibration – to amplify cognitive ability at the individual level and produce collective behaviours that mimic the behaviour of individuals, from signalling danger to locating food for the colony. The duo also describe how social insects reach decisions while searching for new nest sites and transporting large food items through a form of 'polling', which amplifies the individual selection process. However, social insects are also capable of solving problems – such as obstacle negotiation with large pieces of food – though random processes, which yield astounding outcomes that exceed the abilities of the isolated individual. 'The coexistence of these two very different pathways to collective cognition is the novelty of our discussion', says Feinerman.

In one of the most enigmatic of superorganism activities – nest construction – individual ants and termites excavate architectural networks of chambers and shafts that extend tens of metres without the guidance of a blueprint. Andrea Perna from the University of Roehampton, UK, and Guy Theraulaz from CNRS, Toulouse, France, describe nest structures in their review. They say, 'With very few exceptions, underground nests have a tree-like structure' (pp. 83-91). In general, insects that are involved in construction do not share information directly, relying instead on guidance from pheromone-laced building materials, their memories of the construction site and the flow of nest-mate construction workers. The most sophisticated nests are produced by the largest insect colonies, and Perna and Theraulaz explain that these complex structures develop naturally from constantly evolving pheromone distributions and the insect's own body templates, which dictate where material is excavated or deposited.

Evolution of vertebrate social behaviour

Eva Fischer and Lauren O'Connell from Harvard University, USA, argue that, at a basic level, feeding underpins many of the diverse array of social behaviours found in vertebrate species, from mate selection and parental care to foraging in family and social groups. In their review, the two scientists discuss the evidence that many mechanisms that mediate feeding in vertebrates are shared with the circuits that control social behaviour (pp. 92-102). Having listed the neural and hormonal mechanisms through which feeding is mediated, the duo then extrapolate their arguments to the role of feeding circuits in rodent, invertebrate, amphibian and fish parenting behaviour, before discussing how these circuits evolved to influence parenting. Fischer and O'Connell also present evidence that modifications to feeding and foraging circuits in invertebrates such as honeybees and *Drosophila* have led to the evolution of sophisticated social insect behaviour.

Little devil poison frog and froglet, *Oophaga sylbatica*. Photo credit: Elicio E. Tapia.

Within many mammalian species, Allison Perkeybile and Karen Bales from the University of California, Davis, USA, explain that social bonds, which are transmitted across generations, are crucial for survival and reproduction (pp. 114-123). Reviewing our current understanding of how social bonds are formed and transmitted in the best-studied animals – prairie voles and titi monkeys – Perkeybile and Bales explain that the social memory receptors for the hormones oxytocin and vasopressin underpin social memory and work in concert with dopamine reward receptors to establish social bonding. However, they add that the quality of parental care is also a key factor in establishing stable pair-bonds in rodents. Discussing the impact that parenting provided by non-monogamous species – which do not form strong pair bonds – has on hormone production and brain structures in their offspring, the duo says, 'It is clear that variation in maternal care during the first week of life has profound consequences'. Switching focus to the monogamous prairie vole, they describe how good parental care stimulates the social memory receptors, in addition to reducing the level of stress hormones and increasing brain connectivity in the offspring, which is also likely to modify behaviour in later life.

African cichlid fish, *Astatotilapia burtoni*, demonstrate a complex selection of sophisticated social behaviours, from the establishment of dominance hierarchies – resulting from competition for territory, food and mates; to deception, when animals attempt to mislead others about their social status; to the ability to assess when it is possible to ascend the hierarchy (pp. 103-113). Russell Fernald from Stanford University, USA, reviews how DNA methylation plays a major role in male social status by modifying gene expression patterns corresponding to the social rank. He also explains that when a female is offered a choice between her mate and another male having watched the pair duel, the female alters expression of immediate early genes in her brain depending on whether her chosen male wins or loses the fight. Pointing out that changes in social hierarchical behaviour alter selection pressures that will in turn alter the evolutionary pathway, Fernald says, 'Discovering the cellular and molecular substrates for the social skills as described here should lead to a better understanding about how the genome and nervous system can be transformed through social interactions in both the proximate and ultimate sense'.

Concluding the collection of reviews, Ofer Tchernichovski from Hunter College, USA, and colleagues Olga Feher from the University of Edinburgh, UK, Daniel Fimiarz from The City College of New York, USA, and Dalton Conley from Princeton University, USA, focus on social evolution through bird song (pp. 124-132). Together, they describe three forms of song learning that lead to the evolution of a stable song culture: the transition from a continuum of sound production (without clearly distinct sounds) to communication with distinct identifiable acoustic features, otherwise known as signal compression; song learning with the inclusion of errors; and instinctive learning biases that prevent song cultures from drifting over large geographical ranges. The authors then suggest that many parallels can be drawn between social learning in bird song and the spread of information through social networks, showing how social networks with different degrees of connectivity can shape human culture and alter opinion.

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