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Guest editorial

Conflict within cooperation

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Many animals form cooperative societies, but scratch the surface and you will usually find conflict bubbling underneath. Honeybees seem to live in charming, harmonious societies, as they make artisanal honey. But honeybee sister queens will fight to the death to obtain control of a colony; and some workers try to sneakily lay their own eggs, rather than rearing the eggs of the queen [1]. Other workers 'police' this non-cooperative behavior, by eating these eggs laid by workers.

But why do conflict and cooperation go hand in hand? Evolutionary theory gives us the answer to this question, by showing us that the same factors that bring individuals together to cooperate can also put them into conflict (Figure 1).

We can imagine that the interests of interacting individuals could be aligned with a value of anything from 0 to 100%. Alignment could be generated by individuals being genetically related (kin selection). In many cases the alignment of interest will be determined, and could be estimated by the relatedness between individuals, which is a measure of genetic similarity [2]. An extreme case is the effectively genetically identical cells that make up your body, which leads to a 100% alignment of interest.

Alignment of interest could also be generated between non-relatives, if individuals depend upon each other for reproductive success. For example, pea aphids depend upon their Buchnera bacterial symbionts to supply them with amino acids, whereas Buchnera need their hosts to reproduce, so that they can be passed on to the next generation of aphids [3]. Each of these partners do better when their partner is better able to survive and reproduce, and so they have a shared interest in cooperatively helping each other.

At one extreme, with 100% shared interest, there is no conflict and only the potential for cooperation. At the other extreme, with 0% or no shared interest, there is no potential for cooperation, and only potential for conflict. This conflict could be over factors such as competition for resources, such as when individuals compete for food and space, or males compete for mates [4]. For example, when male fig wasps compete for females to mate, they routinely indulge in lethal combat, which can lead to decapitation [5].

In the entire rest of the range, between the two extremes of 0% and 100% shared interest, there is the potential for both cooperation and conflict. Some shared interest (>0%) opens the door for cooperation, but as long as interests are not aligned 100%, individuals can do better by looking after their own interests, and so there is the potential for conflict. This conflict might still just be over some resource, or when there is cooperation, it could be about the form of cooperation. In cooperative societies, individuals could do better by gaining more of the benefits of cooperation, while performing less of the cooperation. For example, in a cooperative breeding vertebrate, like a meerkat, an individual would have a higher fitness if they were the dominant breeder in the group, and others were helping to rear their offspring, compared to if they were the subordinate helper, raising the offspring of others [2].

Consequently, whenever there is cooperation, but the interests of different individuals are not completely aligned, there will be the potential for conflict to evolve. Cooperation and conflict are seen together at all levels of biology from genes within an organism to communities composed of unicellular or multicellular organisms.

Genes cooperate to build organisms, but in some instances genes can manipulate traits, such as sex ratio, to increase their own transmission to the next generation, even when this is costly for almost every other gene in that individual [6]. Social amoebae cooperate to form fruiting bodies, but each cell can benefit from being one of the spore cells that are dispersed, rather than one of the perishable stalk cells that hold up the spores [7].

Bacteria secrete factors that benefit the local group of cells, for example molecules to scavenge iron or digest proteins, and so act as 'public goods'. But there is conflict over who produces the public goods, leading to non-producing 'cheats' that reap the

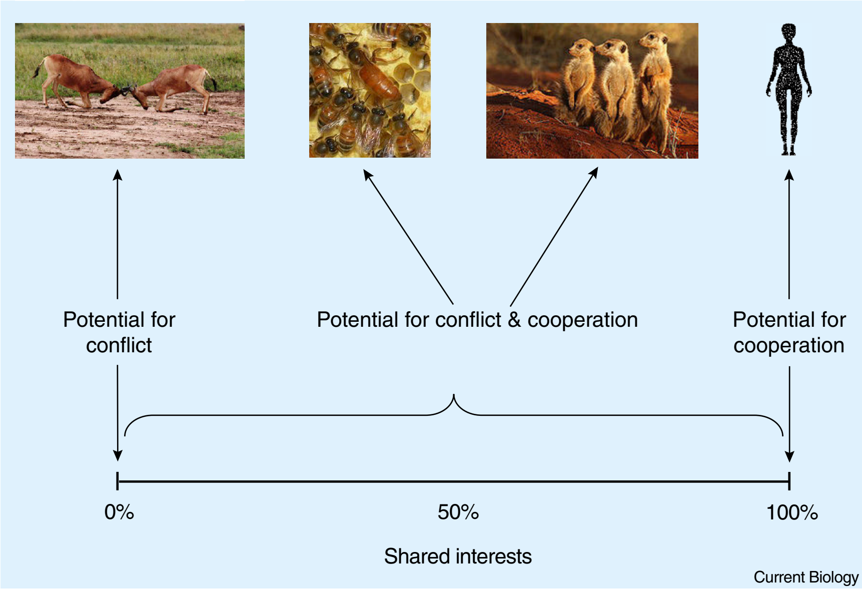

Figure 1. Conflict within cooperation.
Except in extreme circumstances there will usually be potential for both conflict and cooperation between interacting individuals. The pictures from left to right range from cases of 0% shared interest where two hartebeest males compete for territory, to some shared interest such as honeybee workers that rear the queen's eggs, or meerkats that babysit the group's offspring, to effectively 100% shared interest, such as the genetically identical cells that compose a human body (photos: hartebeest: Filip Lachowski (CC BY-SA 2.0); honeybees: Jessica Lawrence, Eurofins Agroscience Services, Bugwood.org (CC BY 3.0); meerkats: Charles J. Sharp, Sharp Photography (CC BY-SA 4.0)).

benefits of cooperation [8]. Bacteria also cooperate to kill. They secrete bacteriocin molecules that kill unrelated bacteria, and so reduce competition for their clonemates, who are immune to the bacteriocins [9].

Males and females join together to raise offspring, but each can be selected to contribute differently to parental care [10]. And there is conflict between these parents and their offspring over how much care to give the offspring [11]. For example, while a foraging bird could be favoured to share its food between its chicks, each chick would like to receive a greater share of that food. And they would be favoured to obtain an even greater share when they are less related to their siblings, and hence have less aligned interests [12].

One of the most exciting aspects of conflict within cooperative societies is that we can often make very clear predictions about when it would occur and the form it should take. Combined with elegant empirical studies, this has led to work on conflict providing some of the greatest success stories of the social evolution literature. For example, the workers in colonies of ants, bees and wasps have been shown to adjust the sex ratio of larvae being reared in the colony with extreme precision, towards the worker optimum, and away from the queen optimum [4]. Social insect workers may be sterile helpers, but they do not blindly help the queen — they still look after their own interests.

An appreciation of this potential for conflict and cooperation has led to a much more nuanced understanding of societies. Except in extreme cases, like clonal groups, assuming that individuals are behaving ‘for the good of the group’ will lead to error [2,13]. Instead, we see individuals trying to maximize their fitness, which can sometimes involve cooperation, but sometimes involve conflict.

The papers in this special issue show where the study of conflict and cooperation is heading. They provide a range of fascinating examples, from genes to complex animal societies, which are fast becoming tomorrow’s success stories. Furthermore, by bringing this work together, this collection of papers illustrates how different study systems offer different advantages to understanding the evolution of conflict and cooperation. For example, with multicellular systems we can more easily record individuals’ behaviours in a group to study cooperation and conflict, while the search for the underlying genes driving these behaviours is more complex. Whereas microbes offer tractable systems in which we can more easily detect the mechanisms underlying the behaviours and when they are driven by gene loss or acquisition, gene mutations, changes in the genomic architecture or regulation [14]. The papers review how we have exploited advances in technology to study sociality in much greater depth, detecting the mechanisms underlying cooperation and conflict at a much finer scale, to determine how the tension between conflict and cooperation plays out in the real world.

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Feature

Uncovering the roots of religion

Religious beliefs can inspire collaboration on enormous scales, as witnessed by monuments like ancient cathedrals and mosques. At the same time, they are also known to fuel conflicts which haunt us to this day. The most powerful and pervasive ‘big god’ beliefs appear to be a relatively late-occurring phenomenon in the evolution of complex societies, as a comprehensive new study suggests. **Michael Gross** reports.

The fire that destroyed the roof and the spire of Notre Dame cathedral in Paris on April 15 united people around the world in their shock and grief at the damage to —and narrowly avoided loss of — an icon of global cultural heritage. The cathedral meant many different things to the many thousands of visitors it attracted. It was a place of worship for some, an architectural marvel for others, and the mascot of a Disney movie as well as a Victor Hugo novel for many.

The design of gothic cathedrals where the weight of the roof and upper walls is channelled outwards by the buttresses implies that the destruction of the roof could have very easily caused the entire cathedral to collapse like a house of cards. The sheer implausibility of people erecting such a gravity-defying monument with the mechanical tools available in the 13th century reminds us that religion is a very strong motivator that can get large numbers of people to cooperate and achieve amazing results.

While Notre Dame is closed for repairs, there are half a dozen other gothic cathedrals around northern France inviting visitors to ponder the question of just how ardently people must have believed in their cause to erect stone arches in the sky with their bare hands.

The project to build Notre Dame was launched around 1163, and construction completed around 1300. During that same timeframe, the same religion also inspired a very different kind of endeavour, namely the crusades against the Muslims in the Middle East. From the Third Crusade (1189–1192)