Guest Editorial

All of life is social

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Sociality means living in groups. Group living intensifies two opposing forces. On one side, proximity exacerbates conflict for local resources. On the other side, cooperation with neighbors may enhance group efficiency and aid in competition against other groups. Starting in the 1960s, biologists made many conceptual advances in understanding the forces of conflict and cooperation that shape social life. That new understanding was applied with great success to honey bees, macaques, and other obviously social, group-living species. Then biologists began to recognize the social history of other types of groups. For example, multicellularity originated through a complex evolutionary history of cellular aggregations, in which the opposing social forces of conflict and cooperation likely played a key role. Similarly, genomes arose through social histories of genetic aggregations and organelle symbioses. Several aspects of multicellularity, of genomes, of societies, and of cognition can be understood only within the social history of conflict and cooperation. This special issue of *Current Biology* presents a series of reviews and primers on sociality and its consequences.

How did multicellularity evolve into the nearly seamless individuals of modern organisms [1]? Slime molds provide some clues about the social problems that had to be solved [2–4]. Slime molds live most of their lives as single cells. Occasionally, local populations of cells aggregate. The aggregation then differentiates into two tissues: reproductive cells that form spores and somatic cells that form a stalk to raise the spores up from the ground. Many labs study this germ–soma differentiation as a model for the molecular biology of development.

Certain slime mold genotypes get into the germline tissue more frequently than other neighboring genotypes in the aggregation [5]. An aggregation with a higher frequency of those that bias their reproductive success leads to shorter stalks and lower total reproductive output: competition for reproduction opposes the cooperative success of the group.

Slime mold aggregations are relatively small, on the order of 10^4 cells. How did multicellularity overcome internal conflicts to allow larger, more complex aggregations to function in a unitary way [1]? Most multicellular organisms develop from a single-cell progenitor, usually a haploid reproductive cell or a diploid zygote. All tissues form a clone derived from the progenitor, thus reducing the chance of competition between different genotypes. By this view, the single-cell stage was a key solution to the social problems of multicellularity [6].

Even with a single-cell progenitor, mutations during development can create genetic variation and conflict within the organism [1]. Many attributes of cellular biology, which originated in single-celled organisms, may have subsequently evolved to repress such conflicts in multicellularity. For example, the DNA repair system, apoptotic controls and cell cycle checkpoint processes tightly regulate cellular birth and death, preventing renegade lineages from growing into uncontrolled tumors. Rigid developmental regulation of the germ–soma separation may reduce the potential for reproductive conflict. Complex systems of self versus nonself discrimination in marine organisms probably originated to protect the multicellular clone from genetic invasion by competing neighbors; those recognition systems may have been the evolutionary precursors of major components of the vertebrate immune system.

Genomes went through a similar social progression in evolution [6,7]. Early genomes suffered unregulated competition within aggregations of genetic material; later genomes repress genomic conflict through the highly regulated patterns of Mendelian transmission. Of course, we cannot directly observe early genomes. But we can study the genetic systems of viruses and bacteria as models of genomes that lack evolutionarily advanced mechanisms to regulate internal competition.

In viruses, defective-interfering genomes arise spontaneously by deletion mutations [8]. The shortened genomes of the defective-interfering particles cannot replicate unless they coinfect a cell with a wild-type virus. Upon coinfection, the defective-interfering genome replicates more quickly and outcompetes the wild type. The coinfected cell produces mostly defective-interfering viruses. Early genomes must have faced the same problems: among multiple copies of an RNA or DNA molecule (chromosome), shortened deletion variants would replicate faster. The genome could not function without some full-length copies, but could not rid itself of the faster replicating deletion mutants. To overcome this problem, genomes required mechanisms to regulate duplication and transmission of chromosomes.

In bacteria, genes are transmitted vertically from parent to offspring via cell division and horizontally from cell to cell via plasmids or bacteriophage [9]. A horizontally transmitted genomic component increases in frequency even if it harms its host genome, as long as any harm to its host is compensated by an increase in its ability to achieve horizontal transmission to other genomes.

Genomes could repress opportunities for internal competition by various mechanisms: they could seal off opportunities for horizontal transmission; they could regulate

copy number of chromosomes; and they could insure that each chromosome had an equal chance of being transmitted to an offspring [6]. These attributes describe Mendelian genetics. In a Mendelian genome, a genomic component, with few opportunities to compete against neighbors, could only enhance success by raising the efficiency of the whole group [10]. In other words, Mendelian genetics arose to regulate internal genomic competition and promote the unity of the genome [11].

Genomic conflicts do remain: meiotic drive arises when one chromosome outcompetes its homolog for transmission; maternally inherited mitochondria of plants sometimes destroy the pollen through which the mitochondria does not transmit; transposons may disrupt genomic integrity [12]. Perhaps as much as one-third of the genomes of some mammals derive from transposons. No one knows how much of the genomic machinery of replication and transmission regulates and imposes the rigid controls of Mendelian genetics. Beyond the genome, much of the genetic material in any modern "individual" often resides in bacterial symbionts, which transmit by variable combinations of horizontal and vertical pathways [13,14].

Kin selection has been the most powerful theory for analysing patterns of conflict and cooperation in all kinds of society — social insect colonies, primate troops, multicell aggregations or genomes [15]. The theory of kin selection explains how genetic variation determines the intensity of conflicting interests within the group and the benefits of group cohesion in competition against other groups [16]. The word 'kin' is used because the shared genetics between relatives usually explains the distribution of genetic variation within and between groups. The more closely related group members are, the more strongly kin selection favors cooperation within the group. Much study of societies turns on the process of kin selection.

I am particularly fascinated by how researchers have recently taken the idea of kin selection, developed originally in the study of animal societies, and applied it to bacteria [17]. For example, many bacteria secrete iron-scavenging molecules, called siderophores. Those molecules bind to iron and can be taken up by bacterial cells. Experimental studies show that, in iron-rich environments, those cells that secrete siderophores have a lower fitness than do non-secretors: secretion imposes a cost on individuals [18]. Typically, any cell in a population can take up a siderophore-iron complex, so the benefit of siderophore secretion accrues equally to all members of the population, whether or not they secrete siderophores themselves. Put another way, individuals bear the cost of secretion, everyone shares the benefit. An individual that does not secrete outcompetes its neighbors and increases in frequency in the population. Yet secretion commonly occurs.

Kin selection provides a possible explanation for this conundrum [18]. Non-secreting individuals gain against their neighbors, but local populations of mostly non-secretors do relatively poorly at extracting resources from the environment. If individuals within groups tend to be genetically similar — if they are kin — then natural selection weights more heavily competition between groups. The more efficient groups, those with more secretors, do better in group competition. The ultimate frequency of secretors depends on the balance between the loss within the group for secretors and the gain of secretors in competition with other groups. The theory of kin selection provides clear quantitative predictions about how changes in genetic relatedness within groups alter the balance and the expected frequency of secretors.

An experimental study [18] varied the level of relatedness within bacterial groups and measured the frequency of secretors in response to several generations of natural selection. The results supported the prediction of kin selection theory: higher relatedness within groups led to greater production of siderophores.

Several other bacterial traits share the distinction between costs borne by the secretors and benefits gained by all members of the local population. West *et al.* [17] list quorum-sensing molecules, antibiotics used in competition against other bacterial species, antibiotic-degradation compounds, immune-modulation molecules, biosurfactants for motility, and certain components of the biofilm extracellular matrix, such as exopolysaccharides and adhesive polymers. In short, much of bacterial life may be influenced by social processes.

I now turn from bacteria to the more advanced end of evolutionary complexity. Human cognition and language developed during a short, spectacular acceleration of brain size and information processing capacity. The human brain rises far above the common allometric scaling between body size and brain size that describes the position of most other animals [19]. Did humans historically have such vastly greater complexity in their problems of foraging and sex than other animals? Or was the social history of humans a major driver of cognitive complexity [20]? As human bands grew larger, how did those groups deal with the problems of internal competition and the need for success in competition against other groups [21]? In the evolution of language, which was more challenging: transmission of a reliable signal, or deception, scenario building, and complex strategic planning in group against group competition [22]?

There is no space to address all of those questions here, so read more about the social history of life in these pages of *Current Biology*.

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Quick guide

Social spiders

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What are social spiders? We tend to think of spiders as aggressive loners, who are happier to eat their siblings rather than live alongside them, but a few hundred of the 38,000 described spider species have truly gregarious lifestyles. At the last count only 26 of these were regarded as non-territorial, permanently social species living in shared webs (Figure 1), whilst dozens form colonies of contiguous, but independent webs that can be permanent or temporary aggregations. Colony size ranges from a handful to tens of thousands.

Where do they live? Spider sociality is widespread and generally considered to have evolved independently in Africa, Asia, Australasia, the Americas and Middle East. Permanently social species are suggested to be phylogenetically apical rather than basal. They are often locally abundant. When Darwin arrived in Brazil he was surprised to observe widespread gregarious habits in the usually 'bloodthirsty and solitary' spiders he found there.

Fortunately for the 30% of people who fear spiders these colonies are sessile, unlike those depicted in Arachnophobia, although the 20 cm (leg-span) spiders starring in that movie were actually social huntsman spiders (*Delena cancerides*) from Australia.

What do spiders do that is social? A broad spectrum of social behaviour is found in spiders. Adults and spiderlings live together in aggregations where they cooperate in web-building, prey capture (Figure 2) and brood rearing. There is an overlap of generations, but the reproductive division of labour characteristic of the eusociality found in ants, bees, wasps and termites is largely absent. Eusociality has only been claimed for one species, *Anelosimus eximius*, in which a large proportion of females are never inseminated and so remain in the nest only as helpers; effectively a non-reproducing worker caste. Division of labour is not a prominent feature of spider societies either, except that in some species larger individuals preferentially carry prey to the main nest, while males contribute little to nest building or prey capture.

If the males do so little aren't they a burden on their groups? Social spiders have a highly skewed sex ratio, where only 8–17% of the colony is male. The source of this skew is unknown, but because sex is

Figure 1. Colonies of the social spider *Stegodyphus dumicola*, in Namibia.

The dense silk nests can contain several hundred spiders and are interconnected with prey capture webs. (Photograph: Trine Bilde.)