

Beyond society: the evolution of organismality

David C. Queller* and Joan E. Strassmann

Department of Ecology and Evolutionary Biology, Rice University, 6100 Main Street, Houston, TX 77005, USA

The evolution of organismality is a social process. All organisms originated from groups of simpler units that now show high cooperation among the parts and are nearly free of conflicts. We suggest that this near-unanimous cooperation be taken as the defining trait of organisms. Consistency then requires that we accept some unconventional organisms, including some social insect colonies, some microbial groups and viruses, a few sexual partnerships and a number of mutualistic associations. Whether we call these organisms or not, a major task is to explain such cooperative entities, and our survey suggests that many of the traits commonly used to define organisms are not essential. These non-essential traits include physical contiguity, indivisibility, clonality or high relatedness, development from a single cell, short-term and long-term genetic cotransmission, germ–soma separation and membership in the same species.

Keywords: organism; organismality; individuality; social evolution; cooperation; conflict

1. COMPETITORS, SIMPLE GROUPS, SOCIETIES AND ORGANISMS

How important is cooperation in the grand scheme of life? We tend to think first of the spectacular social insects like honeybees or leaf-cutter ants, and by extension the simpler social insects and vertebrate societies that most approach them in reproductive cooperation. We might also think of human and other primate societies, whose cooperation does not ordinarily include reproductive specialization, but is remarkable in other ways. Impressive as some of these are, when we consider all three life domains on Earth—Archea, Bacteria and Eukarya with its animals, plants, protists and fungi (Woese & Olsen 1986)—one could argue that this is a pretty meagre showing for cooperation, and be tempted to chalk it up to the Darwinian imperative to compete. One might conclude that cooperation is very difficult and therefore rare. But that is much too narrow a view, for several reasons.

First, we tend to restrict our attention to the organisms that are most obvious or most familiar. If we look beyond them, we find cooperation much more widely. For example, it is now becoming appreciated how often microbes are cooperative (Crespi 2001; Velicer 2003; Foster *in press*). Second, there are some forms of cooperation that we know are common, but that we overlook. Pollination, for example, is a very common form of cooperation between species. And we sometimes forget the sexual bond, which, for all the conflicts it engenders, is an important and pervasive form of cooperation.

Finally, there is another kind of cooperation that we tend to forget because the cooperators have become so

intimate as to blur their boundaries. We are referring here to organisms—not to the societies made up of organisms but to the individual organism itself. We now recognize that there are several levels of organism and that each level was attained by merging formerly separate individuals from a lower level (Buss 1987; Maynard Smith & Szathmáry 1995; Michod 2000). Multi-cellular individuals are cooperative groups of cells, eukaryotic cells are cooperative assemblages of multiple prokaryotic lineages and prokaryotic cells must have emerged by assembly of formerly independent replicators. These major transitions in evolution construct new levels of organism out of separate individuals. Thus, the theory and experience we have accumulated on animal societies over the last few decades turn out to be relevant to truly central questions about the organization of life.

In this paper, we focus on organismality as a social phenomenon. The use of this slightly awkward 6-syllable noun deserves some justification. Buss used ‘individuality’ to mean something similar, a usage that has venerable roots (Huxley 1912). But the indivisibility implied by this word is among the features we want to de-emphasize, and individuality gets us unnecessarily tied up in issues that only philosophers love. ‘Unit of selection’ is relevant, but has been used for both units of heritability and units of interaction. The latter, called interactors (Hull 1980) or vehicles (Dawkins 1982), comes closer to our conception, but may sometimes be used for any phenotypic effect.

Having settled on a term, we should defend the concept, for it has been suggested that little may hang on the concept of the organism (Wilson 2000). That may be true in an instrumental sense—we do not necessarily need to define the organism to do most of our work as biologists (but see Pepper & Herron 2008). But we have in mind something more basic, not something that explains, but something

* Author for correspondence (queller@rice.edu).

One contribution of 16 to a Discussion Meeting Issue ‘The evolution of society’.

that needs to be explained. Probably the first thing that anyone would notice about how life is organized, even more fundamental than species groupings, is that life is divided into organisms. The organism is at least as fundamental to biology as cities or firms should be to economics, or molecules to chemistry. Explaining organismality should therefore be a central task of biology.

What is it that needs explaining? A common approach to defining the organism involves listing characteristics of ‘paradigm organisms’, especially animals, and then trying to decide which combinations of these characteristics are sufficient for organismality when some are missing (see reviews by Santelices 1999; Wilson 1999; Pepper & Herron 2008). The list can include indivisibility, functional integration, contiguity, development from a single cell, membership in a single lineage, genetic uniformity, cotransmission, no partner change and germ–soma separation. Our approach is the opposite. We begin broadly with what we consider to be the essential characteristics of all organisms, and view the other traits as secondary, though potentially important in explaining how organismality was achieved in different taxa.

The most salient feature of organisms is adaptation, the seeming goal-directedness that makes organisms different from merely physical entities. Not all adaptations are organismal. Meiotic drive is adaptive for the drive genes, but not for the individual in which they reside (Burt & Trivers 2006). But, such examples notwithstanding, adaptations do tend to be strongly bundled into what we call organisms. Every organism has numerous adaptations, all directed to the growth, development and reproduction of that organism (and sometimes its kin). We suggest that the essence of organismality lies in this shared purpose; the parts work together for the integrated whole, with high cooperation and very low conflict. Specifically, the organism is the largest unit of near-unanimous design; the qualifying ‘near’ is required because some conflicts, like meiotic drive, probably remain in all organisms. All organism concepts emphasize function and integration; ours differs in stressing unanimity, and in ignoring other traits. Our definition is a social one; the organism is simply a unit with high cooperation and very low conflict among its parts. That is, the organism has adaptations and it is not much disrupted by adaptations at lower levels.

A related argument for the organism (or super-organism) as the unit of adaptation has recently been advanced based on a formal analysis of the relationship between the potential for selection and adaptation (Gardner & Grafen 2009). Our approach is complementary in the sense that we start at the empirical end and ask what kinds of entities might be considered organismal. It differs however in focusing on actual, rather than potential, cooperation and conflict. This distinction between potential and actual conflict has been proved fruitful in the study of insect societies (Ratnieks *et al.* 2006). We believe that organisms should be defined by what they actually do, and only subsequently explained by the potentials engendered by factors like high relatedness and suppression of conflict.

One consequence of the decision to focus on actual behaviour is that we consider cooperation and conflict separately. In theory, the same factors that lead to high potential cooperation also lead to low potential conflict, but in reality, the two are far from perfectly correlated. For example, a clone of non-social aphids has zero potential conflict and great potential cooperation because their genetic interests are identical. In reality, they do show little conflict, but do not show much cooperation, presumably because there is rather little they can usefully do. At the other end, we have human societies and mutualistic groupings where there is extensive cooperation among non-relatives in spite of great conflict.

As a framework, we use a graphical representation of societies or social groups (figures 1–3). It provides a fourfold classification, although it is really a continuous classification in two dimensions: the extent of cooperation and the extent of conflict. We have plotted conflict on a decreasing scale in order to put the most organismal of groups in the upper-right quadrant. These traits are not quantified in a manner that justifies numerical scales. But they suffice for our qualitative and far-from-perfect judgments of where different kinds of groups fall (figures 1–3). We hope this scheme provides a useful way to think about the issues surrounding organismality.

We show this continuous space of sociality divided by two lines. Our intent is to divide the space in a way that separates organismal groups from others; we view groups placed close to the lines as hard to classify. Conventional organisms fall somewhere in the upper-right quadrant, with sufficiently high cooperation and sufficiently low conflict. In the opposite quadrant reside the many groups that are unlike organisms in terms of both cooperation and conflict—too little cooperation and too much conflict. We call these competitors. At the lower right are ‘simple groups’ that have little enough conflict to be considered organisms, but lack the degree of cooperation required. Finally, we limit the term ‘societies’ (upper left) to groups, like the human groups for which the term was originally coined, that have high cooperation, but mixed in with considerable conflict.

Our goal in this paper is to survey the landscape of actual conflict and cooperation, a first step in the process of explaining it in terms of theory, which would include, but not be restricted to, the amount of potential conflict. In practice, however, our knowledge of potential conflicts will sometimes colour our judgments when too little is known of actual conflicts.

2. GROUPS OF CELLS

The cooperation/conflict space can be explored at several different levels (figures 1–3). We begin with groups of cells where the issue of organismality is most obvious. Figure 1 shows how we could place some of these groups in the cooperation/conflict space. Here we are considering conflicts among cells only, leaving conflicts among genes within cells for later discussion.

The classical organisms are the bilaterian animals; discrete, with highly specialized and integrated

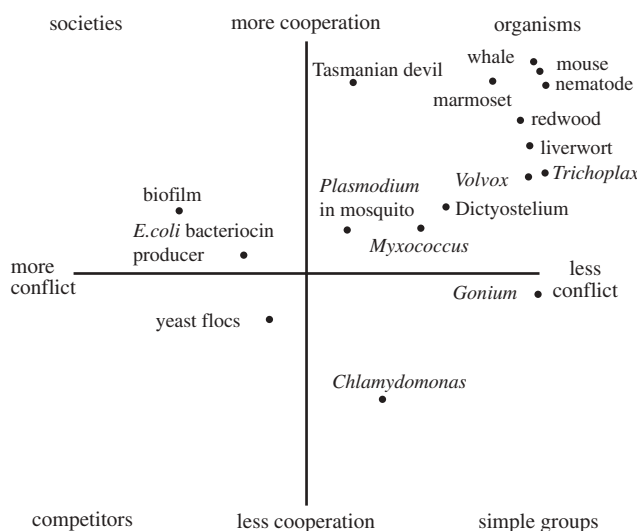


Figure 1. Cooperation and conflict in groups of cells. Only cellular conflicts are considered here, but within-cell conflicts are discussed in the text.

organs, tissues and cell types (Davidson *et al.* 1995). Each develops from a single fertilized cell, leading to an essentially genetically uniform group. This is why we have plotted them at the extreme low-conflict end. The only obvious cell conflicts must therefore involve new mutations.

Traits like germline sequestration might have evolved to control selfish mutations (Buss 1987; Michod & Roze 1999), though the single-cell bottleneck may have been sufficient by itself (Queller 1997). Current conflicts are largely limited to cancer, though in some ways cancer seems like any other somatic mutation, in that it will be eliminated in the single-cell bottleneck leading to the next generation. But the replication of cancer cells does lend them a selfish social dimension, however short-lived (Frank & Nowak 2004). We have therefore placed large, many-celled organisms, like whales and redwoods, as having slightly more conflict than smaller ones. More serious conflict occurs only when there are violations of the single-cell bottleneck rule. In marmosets, cells regularly mix between fraternal twins *in utero*, and the adults can be complex chimeras that may have some conflict (Ross *et al.* 2007). Conflict that is a threat to organization at the organismal level arises if a cancer is transmissible, as in the fatal facial cancer of Tasmanian devils (*Sarcophilus harrisii*; McCallum & Jones 2006). This case points out that the single-cell bottleneck is not a sufficient explanation for organismal cooperation in animals; one also needs the ability to exclude foreign conspecific cells.

We rank plants (redwoods and liverwort in figure 1) somewhat higher for conflict than most animals because growth from a multi-cellular meristem offers greater potential for competition among cells (Pineda-Krch & Lehtila 2004), though here we are speculating that this leads to some actual conflict. We also rank plants a bit lower for cooperation because their semimodular nature sometimes means many interactions are more local than global. Nevertheless, plants are still clearly organismal.

With little cellular conflict in clonal organisms, their position depends more on the extent of cooperation. In the well-known series of volvocine algae, *Volvox* is organismal, with cells and strong differentiation between reproductive and vegetative cells (Herron & Michod 2008). *Gonium*, with eight to 32 undifferentiated cells that cooperate in limited ways, such as coordinating phototaxis, might better be regarded as a simple group. *Chlamydomonas* represents the end of the spectrum occupied by many other single-celled organisms. Their nearest neighbours are presumably often not clonemates, and they may have little cooperation or overt conflict if they are sufficiently dispersed.

However, one of the most spectacular recent developments in the field of social evolution is the growing realization of how social many unicellular microbes are (Crespi 2001; Velicer 2003; West *et al.* 2006; Foster *in press*). The pinnacles of sociality among microbes may be the curiously parallel life cycles of the eukaryote *Dictyostelium* (Queller *et al.* 2003; Shaulsky & Kessin 2003) and the prokaryote *Myxococcus* (Velicer & Stredwick 2002). In each, when feeding cells starve, they aggregate and go through a developmental process that results in fruiting bodies where a fraction of the cells survive as hardy spores. It is somewhat easier to make the case for organismality for *Dictyostelium* fruiting bodies because a fraction of the cells (approx. 25% in *Dictyostelium discoideum*) give up their lives to form a stalk that enhances spore dispersal. In *Myxococcus xanthus*, it is less clear why as many as 90 per cent of the cells die during fruiting body formation (Wireman & Dworkin 1977). One the other hand, *Dictyostelium* is more solitary in the remainder of the life cycle, while *Myxococcus* is very social during that time. It is a swarm feeder, effectively hunting in packs (Velicer 2003).

The amount of conflict in these two organisms deserves further study, but it may be minimal enough for them to qualify as organismal. Because fruiting bodies form by aggregation, there is considerable potential conflict, at least if unrelated cells commonly aggregate. In both *D. discoideum* and *M. xanthus*, we know that there is considerable genetic potential for cheaters that reap the benefits of fruiting while letting others pay the costs (Velicer *et al.* 2000; Santorelli *et al.* 2008), some of which could destroy sociality (Velicer *et al.* 1998; Ennis *et al.* 2000; Gilbert *et al.* 2007). But actual conflict may be rather low. In *Dictyostelium*, there is some separation between clones during fruiting (Mehdiabadi *et al.* 2006; Ostrowski 2008), but it is incomplete and chimeras do form in the laboratory. However, fruiting bodies from the wild are known to be mostly, though not exclusively, clonal.

An indication of the more general importance of social cooperation is that it turns out to be significant in any microbe that is studied with sufficient intensity. *Escherichia coli* and *Saccharomyces cerevisiae* were chosen as model systems for their ease of study. We tend to think of them both as independent cells that grow nicely in broth, which they are, but they also have cooperation, which may be particularly important in more natural environments. For example, *E. coli*

often makes biofilms in which cells are held together in a common matrix (Reisner *et al.* 2006). Under low-nutrient conditions, *E. coli* groups can undergo a coordinated transition to a stationary phase in which growth ceases, avoiding a tragedy of the commons, though there are mutants that cheat and grow faster, something that tends to be advantageous only when rare (Vulic & Kolter 2001). Many *E. coli* clones produce bacteriocin toxins that kill the producing cell and nearby non-clonemates, to the benefit of clonemates (Kerr *et al.* 2002).

The budding yeast *S. cerevisiae* also has multiple cooperative behaviours. As with many microbes, some products are secreted in ways that benefit neighbours. Secreted invertase hydrolyses sucrose, part of which is captured by the secreter, but as much as 99 per cent of it goes to others (Greig & Travisano 2004; Gore *et al.* 2009). Under certain kinds of stress, some yeast form protective clusters called flocs, in which the cells tightly adhere, and protection is offered by both the physical barrier of the outside cells and physiological changes (Smukalla *et al.* 2008).

With their modest array of cooperative behaviours, mixed presumably with some conflict, it seems reasonable to regard *E. coli* and yeast as modest societies. But, of course, the placement would depend on the kind of group. A yeast floc would be closer to organismal than yeast growing in an exponential phase in broth. An *E. coli* group consisting of mixed killers and victims would have to be considered competitive, but the killer clone considered by itself is an altruist that gives its life for relatives. The placement of other microbial species on our axes is even more problematic because we have an even less complete picture of the range of their behaviours. But it is clear that the kinds of cooperative behaviours we see in *E. coli* and yeast—secretion of public goods, biofilms, bacteriocin toxins—are quite widespread (Crespi 2001; Velicer 2003; West *et al.* 2006; Foster *in press*).

Microbial groups are often dispersed and unclearly bounded, which may work against them becoming organismal. Biofilms are at least contiguous, and may sometimes be organisms, but we need more information as to their balance of cooperation and conflict (Xavier & Foster 2007). For more dispersed microbes, quorum sensing often precedes activation of cooperative pathways, and the limit of the group may be viewed as those who sense the quorum.

One case where contiguity may not be necessary for organismality involves groups that live inside another organism. This gives microbes the potential for action at a distance; if they can affect the host, then they can affect each other. For example, the malaria parasite *Plasmodium falciparum* manipulates its mosquito host, benefiting all the parasites in the same mosquito. In the infectious stage, infected mosquitoes bite more often, mediated in part by the parasites' interference with the enzyme apyrase that the mosquito uses to keep its victim's blood from clotting (Koella *et al.* 1998). In the pre-infectious stage, at least in *Plasmodium yoelli*, the parasites have the opposite effect of reducing the mosquito's propensity to bite, thus avoiding danger until the parasites are ready (Anderson *et al.* 1999). When you factor in

suppression of the host immune system and reduction in host fecundity, which preserves resources for the parasite (Lefèvre *et al.* 2006), an argument can be made for organismality. This high cooperation occurs with the high, but less than perfect, relatedness of *P. falciparum* within a mosquito (Razakandrainibe *et al.* 2005). Given the widespread incidence of host manipulation among other parasites (Thomas *et al.* 2004) and the fact that some of them will generally have clonal infections, we expect that such dispersed organisms are probably common. Similar effects can be achieved via beneficial effects on the host, but we will consider these later as parts of possible mutualistic organisms.

3. GROUPS OF GENES IN CELLS

Replicating molecules getting together in cells was presumably one of the early steps in the evolution of life (Koonin & Martin 2005). That transition occurred so long ago and is so fixed that we hesitate to say more than that it is an important example of unrelated replicators becoming organismal. However, issues of cooperating genes remain. The general argument about *Plasmodium* being organismal can easily be extended to many viruses. Scientists who focus on metabolism argue that its absence in viruses means that they are not even alive. Evolutionary biologists tend to disagree, because viruses evolve by natural selection. Whether alive or not, they can be organismal by our definition. A virus contains a small set of genes, each of which performs a key task in manipulating the host into making virus copies. Although cheating is possible in viruses, particularly in mixed infections (Turner & Chao 1999), it seems likely that many function as fully cooperative units.

Conflict among genes is also an issue for larger organisms. In our discussion of clonal multi-cellular organisms above, we considered only conflict among the cells. However, there is sometimes substantially more conflict among the genes within cells (Hurst 1998; Hurst & Werren 2001; Burt & Trivers 2006). With sufficient information, we could add this kind of conflict in figure 1, or alternatively construct another figure that shows cooperation and conflict at the genetic level in those organisms, but we will be content to make some general points, most of which concern sex.

The first is that we should not forget what a cooperative venture sexual reproduction is. Here we are referring not to the cooperation of the parents, which we will treat later, but of the cooperation that results after two unrelated sets of genes are put together in the zygote. We think of organisms as being built by genetically identical lineages of cells, and we tend to forget that, with every sexual event, an organism is initiated by the horizontal amalgamation of two cells that have great potential conflict but little actual conflict. Clearly, high relatedness is not essential for organismality.

The potential for conflict among such unrelated genes is very high, but it is normally strongly limited in several ways. The fairness of meiosis normally limits within-organism competition between alleles.

Selfish coalitions among alleles are limited by recombination and by the fact that genes are not usually marked by parent of origin. Nevertheless, some conflicts do arise when these conditions are violated. Meiotic-drive alleles gain by defeating the fair meiosis (Lyttle 1991). Some can impose significant costs on the organism, but spread nevertheless because of within-organism advantage. We do not know how common meiotic-drive mutants are because many may sweep to fixation, at which point they are unobservable. However, fixation is most likely when the drive imposes little cost at the organismal level, so even if these are common, they do not destroy organismal cooperation.

Conflicts can also occur when parental genes are differentially marked by methylation. Maternally and paternally derived genes (matrigenes and patrigenes; Queller 2003) may be selected differently if they have different relatedness coefficients (Haig 2000). There is considerable evidence that patrigenes fight harder for their embryo than matrigenes when the resources gained come at the expense of half siblings (who share matrigenes but not patrigenes). Oddly, such within-organism conflicts are predicted to be most diverse in those paragons of cooperation at a higher level, social insect workers (Queller 2003), though these predictions remain to be tested.

Perhaps the most pervasive genetic conflicts within individuals come from selfish DNA, like transposable elements. In asexual organisms, these conflicts tend to be small because they are vertically inherited. But in sexual organisms, the selfish elements can move horizontally from one lineage to another and can therefore spread more readily (Smith 2001). If we were to use a majority-rule criterion, many eukaryotes might not be considered organismal; about half the human genome is derived from transposable elements (Lander *et al.* 2001). However, we use actual conflict as the criterion, and most of these transposons are inactive and presumably not very costly, and some may perform useful functions (Lander *et al.* 2001). High costs do occur in periods when elements enter a virgin territory, as when the *Drosophila melanogaster* p-element entered new populations, until suppressors evolve (Adams 1981).

The main lesson here is that the significant conflicts occur in undoubted organisms, so we cannot use the mere existence of conflict to rule out organismality of other types. In fact, selfish DNA may pose greater problems for more complex organisms because they tend to be larger, with smaller population sizes and weaker between-organism selection. High cooperation and low conflicts do not go strictly hand-in-hand; sometimes high cooperation gives room for conflicts to operate without doing too much damage.

4. GROUPS OF MULTI-CELLULAR INDIVIDUALS

Multi-cellular individuals make up the most familiar groups and societies. Figure 2 shows tentative placements of some groups of multi-cellular individuals. Most of the groups that are the topic of this symposium are societies with complex mixtures of cooperation and conflict. *Polistes* wasps and naked

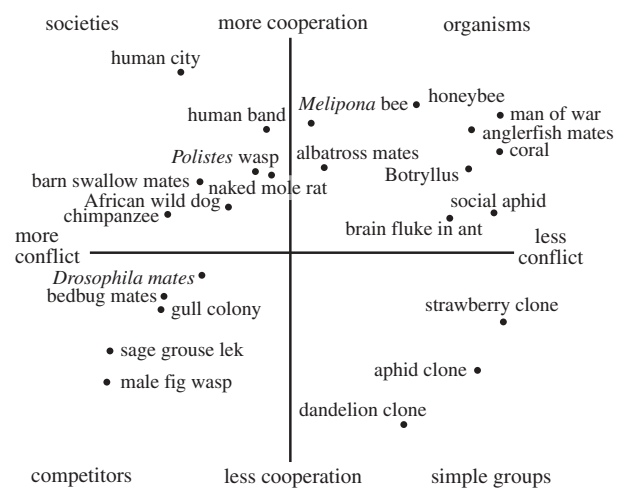


Figure 2. Cooperation and conflict in groups of multi-cellular individuals. Only conflicts between individuals are considered.

mole rats (*Heterocephalus glaber*) have sophisticated cooperation that includes food sharing, group defence, nest building and cooperative brood care of the progeny of one or a few group members. Yet, they are also driven by conflicts. The reproductive position is coveted and subordinates have to be kept in place, often by force or the threat of force. Other cooperative breeders have varying degrees of cooperation and conflict.

Humans fall in this category. Humans are the most successful cooperators; a human city is arguably far more cooperative and integrated than groups of any other species, but that is not sufficient to make it organismal. It is far too full of conflicts. More traditional human bands cooperate in less sophisticated ways but may have less conflict. With numerous ties of both direct and indirect reciprocity, strong between-group competition and within-group homogenization by cultural norms, such bands may approach organism status, though in our view they probably still have too much conflict.

Are there groups that, given our definition, ought to be considered organismal? The question is obviously not ridiculous once it is recognized that these organisms themselves evolved out of groups several times over (Buss 1987; Maynard Smith & Szathmáry 1995). Perhaps, the easiest case to argue is one like the Portuguese man o'war (*Physalia physalis*). Although it is commonly viewed as a colony of polyps, it is hard to deny its organismality in any functional sense. It is a clonal unit, with polyps budding from other polyps in a regular developmental sequence, and remaining attached. The polyps are quite specialized, with some forming a sail for locomotion, others making tentacles to capture prey and others specialized for digestion. All these work on behalf of the polyps that are specialized for reproduction. The whole cannot function without the parts. No conflict is expected among the parts, and as far as we know, none exists.

Somewhat less organismal are colonies of the tunicate *Botryllus schlosseri*, which as a chordate is a close cousin of ours. The colony is made up of perhaps 20

zooids, each quite like a solitary tunicate with its own gut, heart, nervous system and gonads. But the colony members share a common tunic and a common cloaca and an excurrent siphon. Moreover, there is a vascular system connecting the zooids. Again colonies form by budding, but they can also fuse with genetically similar, but not necessarily identical, colonies. When such chimeras form, there can be conflict because sometimes one partner takes over the gonadal tissue of the other.

These colonies share two features—contiguity and genetic identity—that make it easy to view them as organisms, but we view neither as definitive. It has been suggested that an aphid clone or a dandelion clone ought to be considered to be individuals, but we do not consider them to be organisms. Though there is no potential conflict among members of a dandelion clone, they do little or nothing for each other. Indeed, though we have placed them among simple groups, dandelion clones may really be competitors. The units of this ‘individual’ are unattached, being derived from apomictic seeds, and unless they have some mechanism to recognize clonemates, will compete with them just as much as with non-relatives. Plant clones that remain connected, like strawberries, probably have a greater claim to being organismal units, but unless there is considerable integration, we would argue that they are not organisms. If, for example, resource transfer is mainly limited to the establishment of new ramets, the ‘adult’ ramets are best considered separate organisms that reproduce. An aphid clone that remains bunched may be somewhat more cooperative than separated dandelions, for example in evolving warning colouration, but as the level of cooperation appears small, we would not classify such clones as organisms. In contrast, social aphids, where some individuals specialize as soldiers and defend the colony, usually inside a plant gall, could be considered organisms. But even here the cooperation seems mostly limited to defence and is less sophisticated than social insects like *Polistes*. Such colonies may include a small amount of conflict, as mixing with other clones occurs.

The social aphids also raise the question of contiguity. Though usually confined to a gall, the aphids are not attached in the manner of a conventional organism, but we do not consider that grounds for excluding their colonies as organismal because our working definition concerns only the degrees of cooperation and conflict. However, the best cases to argue this point are not the social aphids, with their fairly rudimentary organization, but some of the highly eusocial insects, such as the honeybee (*Apis mellifera*). There is in fact a long tradition of recognizing certain social insect colonies as organismal (Wheeler 1911; Seeley 1989; Wilson & Sober 1989; Strassmann & Queller 2007; Hölldobler & Wilson 2008). Wheeler’s (1911) use of the term ‘organism’ has been largely supplanted by ‘superorganism’, but we concur with Wheeler’s usage because we have come to learn that all of our familiar organisms are superorganisms. If superorganism is meant to highlight the common features of high cooperation, low conflict and unanimity of action, why reserve that term for the top level only? If instead

the intent is to imply that these are somehow different, that they have not quite reached the level of organisms, we really ought to call them quasi-organisms.

A honeybee colony includes tens of thousands of workers. Every aspect of colony life—foraging, brood care, defence, nest construction—is coordinated by communication and social feedbacks towards the end of promoting the queen’s reproduction. The glue is not adhesion molecules and intercellular signals, but attachment to a particular place, pheromones, chemical recognition cues, as well as various visual, tactile and smell signals of work done and undone.

In arguing for organismal status for honeybee colonies, we are not only arguing for organisms with unattached individuals, but also that those individuals need not be genetically identical. By accepting the eukaryotic cell as an organism, we have already acknowledged that genetically distinct partners can become organismal. The genetic differences in a social insect colony lead to potential conflicts, but in honeybees, the actual conflicts appear to be very small (Ratnieks *et al.* 2006; Strassmann & Queller 2007). New queens fight to the death, but at little cost to the colony. Occasionally a worker will lay an egg, but this is kept rare by the effective policing of other workers who eat such eggs (Ratnieks & Visscher 1989). These seem to have as little effect on organismal function as some of the genetic conflicts in conventional organisms (see below).

Although honeybees are the best studied social insect, it seems likely that many others, especially some ants and termites, approach or attain similar levels of cooperation and integration and should also be considered organismal. Some, however, have sufficient conflicts to make this status questionable. Stingless bees of the genus *Melipona*, among the honeybee’s closest relatives, have high degrees of cooperation but offer an interesting contrast (Engels & Imperatriz-Fonseca 1990; Peters *et al.* 1999). In some species, workers commonly compete to lay their own eggs, and these are not effectively policed (Tóth *et al.* 2004). Moreover, because all larvae are given about the same amount of food, they are not forced into a worker role. As a result, 10–20% opt to become queens, even though a new queen is only rarely needed to replace the old one or to found a new colony (Wenseleers & Ratnieks 2004). These selfish superfluous queens are ultimately killed by workers, but their production must exert a significant cost to the colony. We therefore place *Melipona* near the organism–society boundary.

As we argued above for microbes, another category of separated organisms comes from groups of parasites. The brain fluke *Dicrocoelium dendriticum* parasitizes snails, ants and sheep. When an ant ingests a cyst left by a snail, the hundreds of juvenile flukes adaptively divide labour. Most encyst in the haemocoel but one invades the suboesophageal ganglion, causing the ant to climb up a blade of grass where it can be eaten by a sheep (Moore 2002). The ganglion fluke dies, but by manipulating the host, it benefits the rest. Provided there is also little or no conflict among the flukes, this level of cooperation probably qualifies as organismal. The ant of course is not part

of this organism; its adaptations are to produce new ants, and to try to avoid being eaten.

A final category that should be considered is mated pairs. Mating itself is a cooperative act, but it typically also involves conflict. The conflict is extreme in bedbugs (*Cimex lectularius*), where insemination takes place through the body wall of the female (Stutt & Siva-Jothy 2001), and it can take more subtle forms, such as a *Drosophila melanogaster* male chemically inducing his mate to increase her short-term reproduction at the expense of her lifespan (Chapman 2001). Because of the higher cooperation involved in joint parental care, we classify barn swallow (*Hirundo rustica*) mates as societies, but they still have considerable conflict, including infidelities and mate switching (Møller 2002). The whole tale of sexual conflict is too vast to be covered here (Arnqvist & Rowe 2005), but we should consider cases where conflict is minimal. Arguably, albatross pairs that mate for life, after an elaborate and extended courtship, could be considered organismal. We would need to see whether even the low probability of partner change or loss leads to conflict in pairs. We would also need to consider the impact of extra-pair copulations, which do occur, but which seem not to affect pair bonds—females do not seem to seek or benefit from them (Jouventin *et al.* 2007). The clearest cases, however, are when mates fuse. For example, in some, but not all, species of anglerfish, a dwarf male becomes attached for life to a female (Pietsch 2005). He bites onto the female, and outgrowths from both the upper and lower jaws, which are apparently unsuitable for normal feeding, eventually fuse with the female, with apparent vascular connections to feed the male. Neither sex becomes reproductively active unless attached to the other. Such males are sometimes called ‘parasitic’ but in fact they seem to serve cooperatively as male gonads, without any known conflicts with the female, and with few expected in those species where one male is the norm.

5. MULTI-SPECIES GROUPS

We do not generally think of organisms consisting of two species. But they are possible in principle if we employ a functional definition of high cooperation and low conflict. And there is the precedent that everyone accepts. The eukaryotic cell comprises the original cell and the mitochondrion, likely to have originated as an alphaproteobacterium related to *Rickettsia* (Margulis 1970). Plastids, including chloroplasts, came from cyanobacteria in a similar fashion. A long evolutionary history of cooperation has resulted in physical intimacy, private partnership, complete physiological interdependence and division of function. Neither exists without the other, and mitochondria and their host cells speciate together. Inheritance is not identical because mitochondria are usually inherited only through the maternal line. This difference makes some residual conflict of interest possible, particularly with regard to sex allocation. For example, mitochondrial genes cause male sterility in plants (Frank 1989), although most mitochondrial genes do things that are good for the host.

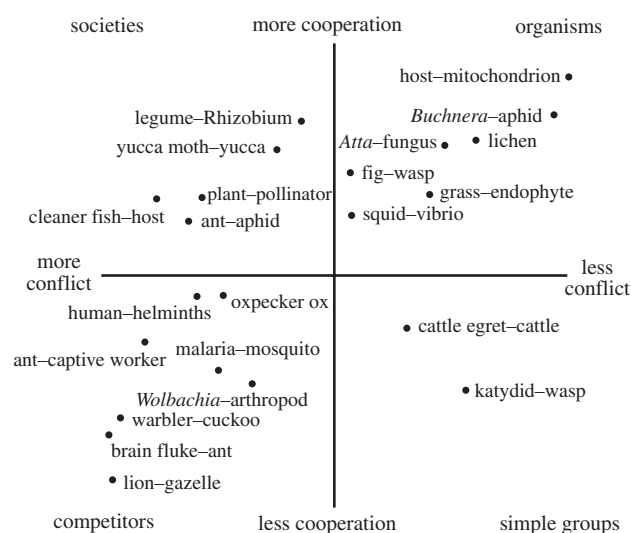


Figure 3. Cooperation and conflict in two-species groups.

This widely accepted precedent means we should ask how many other organisms have been formed from multiple species. Of course, most two-species interactions are not organismal. Some have low enough overt conflict but do not have sufficient cooperation. These are often simple byproduct mutualisms (Sachs *et al.* 2004). Katydid associates with wasp nests during the day, presumably gaining protection from the bellicose wasps (Downhower & Wilson 1973). Cattle egrets (*Bubulcus ibis*) profit from cattle movements that stir up insects and also remove ticks from the cattle (Fogarty & Hetrick 1973). Clearly, the egrets obtain more food when cattle are present, and there is little cost (Burger & Gochfeld 1982). But both can survive independently. Red-billed oxpeckers (*Buphagus erythrorhynchus*), by contrast, are obligate on large African mammals, but they are parasites, not mutualists, and take more blood, mucus and wax than ticks and parasites (Weeks 2000). However organismal the brain flukes may be in their manipulations of the host, the host is not part of that organism because it has not evolved to cooperate. Most host–pathogen and predator–prey relationships would fall in this category. So would socially parasitic relationships like cuckoos and their warbler hosts, or ants and the captive workers (sometimes called slaves) from other species (Brandt *et al.* 2005; Krüger 2007).

There are of course many mutualistic species pairs that perform essential services for each other. The question is how much ongoing conflict there is and which, if any, have so little conflict that they are essentially organismal. Conflicts are readily apparent in many of them (Herre *et al.* 1999; Bronstein *et al.* 2006; Douglas 2008). Cleaner fish perform the essential service of removing parasites from their clients, but also cheat by taking client tissue (Bshary & Grutter 2002; Bshary & Schäffer 2002). Legumes are highly dependent on associated *Rhizobia* bacteria for nitrogen, supplying carbon compounds in return, but multiple bacterial genotypes associate with every plant and conflicts ensue (Sachs *et al.* 2004). Plant sanctions—cutting off oxygen to weak nitrogen

suppliers—helps keep the bacteria in line, but the conflict involved is probably enough for them not to be considered organismal, despite the intricate cooperation (Kiers & Denison 2008; Sachs & Simms 2008). Many flowering plants are completely dependent on animal pollinators to differing degrees of specificity (Johnson & Steiner 2000). The pollinator gets food in return for transferring pollen, but there are often conflicts over how long to stay on one flower or plant, how much pollen the pollinators should take for themselves and how far the pollinator should travel (Bronstein 2001). Interestingly, it can sometimes be the very diversity of partners that stabilizes mutualisms because the optimal partners can be chosen repeatedly (Foster & Kokko 2006).

However, we believe there are mutualistic associations, other than the eukaryotic cell, that should be considered organismal. At the very least, there are other endosymbiotic bacteria that live inside host cells and reproduce along with them. Some two-species organisms involve bacteria that are housed in a small minority of the host organism's cells: the bacteriocytes. *Buchnera aphidicola* produces essential amino acids for its aphid host and also migrates to ovarian cells for vertical transmission (Wernegreen & Moran 2001; Moran 2007). *Buchnera aphidicola* has a tiny genome, under 650 kb, specialized on what aphids cannot make, while many gene products needed by the symbiont are now made by the aphid, further binding their interests. Some potential conflicts remain over reproduction, but the aphid seems to effectively limit symbiont competition, so that little actual conflict occurs (Frank 1996). Acquiring functionality by adopting a bacterium intracellularly has happened repeatedly in insects, particularly those that ingest plant sap (Moran 2007). Many of these cases can be viewed as two-species organisms. However, some show greater signs of conflict and some endosymbionts, like *Wolbachia*, manipulate their arthropod hosts in various ways and do not generally provide any advantage (Charlat *et al.* 2003).

Let us consider a range of possible organisms with decreasing physical intimacy. First, symbionts need not be intracellular. The term symbiosis was first applied to lichens (Sapp 2004), an ancient symbiosis, seen in a 600 million year old fossil (Yuan *et al.* 2005). Lichenized fungi have captured algae (85%), cyanobacteria (10%) or both (4%) to provide carbon (Honegger 1998), which usually grow together via coordinated meristems (Sanders 2006). The fungal partner often optimizes exposure to light, and maintains moisture for the photosynthesizing partner, a relationship that makes lichens the first colonizers in many harsh habitats and dominant in 8 per cent of habitats (Honegger 1998). The fungi at least have lost the ability for independent existence (Lutzoni *et al.* 2001). Sometimes lichenized fungi and their partners are codispersed as fragments of the lichen thallus, but this is not obligate (Nelson & Gargas 2007). Many different fungal species use the same species of algae, or cyanobacteria, and they have not cospeciated (Piercey-Normore & DePriest 2001; Hyvärinen *et al.* 2002; Zoller & Lutzoni 2003). Yet it is hard to argue that lichen symbioses have less than organismal levels of cooperation. Little work seems to have

been done on possible conflicts, though it seems the fungus has a controlling role.

Another plant–fungal association that might sometimes be organismal are certain grass–endophyte mutualisms. Endophytes confer resistance to herbivores, particularly under drought conditions (Clay *et al.* 2005) and are commonly transmitted vertically through seeds, though they can be lost at several different life-stage transitions (Afkhami & Rudgers 2008).

Other organismal mutualisms may be even less connected. Although most pollination mutualisms are not nearly organismal, a few specialized ones may approach it. Specialization is particularly common in nursery pollination systems (Dufay & Anstett 2003) where pollinators lay eggs on the plant. Moths that pollinate both senita cacti (Fleming & Holland 1998) and yucca (Pellmyr *et al.* 1996) provide specialized pollination services, but then exact a cost by parasitizing seeds. Fig wasp pollinators go one step further by both pollinating and having their offspring transport pollen away from the same inflorescence, thus giving the fig an incentive to raising wasps. This mutualism has persisted for at least 60 million years and has diverged into over 800 species of figs and a corresponding number of symbiotic wasp species (Silvieus *et al.* 2007; Rønsted *et al.* 2006). Cospeciation is very close for figs and pollinator wasps, though there is some evidence that the wasps speciate first, and the figs lag behind (Silvieus *et al.* 2007; Herre *et al.* 2008). By contrast, figs and parasitic wasps that are just as dependent on figs do not show evidence of cospeciation (Silvieus *et al.* 2007).

Conflict between fig and pollinator wasps exists but is usually controlled. Each wasp larva destroys an ovule, amounting to around half of all ovules (Herre 1989). Variable style length may be the fig's way of avoiding excessive loss of ovules, though this may be more because of the increased handling time than because they are unreachable by the wasps (Yu *et al.* 2004). Figs may limit access to syconia to one or a few pollinators, thus limiting competition, including the production of excess sons, which are wasteful for the fig. Experiments show that deposition of pollen increases wasp success by some mechanism not involving fruit abortion (Herre *et al.* 2008). Male success of the fig correlates with the number of wasps produced (Herre 1989). It may be that the interests of the figs and pollinators are sufficiently aligned to consider them organismal.

Vertical cotransmission must be helpful in evolving organismality in two-species systems, but is it essential? Many highly developed mutualisms involve symbionts acquired from the environment. Bobtail squid are dependent on *Vibrio fischeri* bacteria for their light production, which allows them to camouflage themselves from predators lower in the water column (Nyholm & McFall-Ngai 2004). The squid are not born with their bacteria but instead take them up in a highly specific and coordinated process involving squid structures that have evolved just for this purpose, the uptake of the preferred bacterium, and not the thousands of others (Visick & McFall-Ngai 2000; Visick & Ruby 2006). Every morning, the squid physically expels 90 per cent of the bacteria (Visick & McFall-Ngai 2000). This appears to keep

the bacteria in an active growth phase, which is when they best luminesce (Visick & McFall-Ngai 2000). We need further study of conflict in this and other systems that acquire their symbionts, but it is possible that these might be considered to be organismal.

As with other organisms, mutualistic ones do not necessarily need to be physically cohesive. Granting that social insect colonies can be organismal, the boundaries of that organism could include other species. *Atta*, a fungus-growing ant, is entirely dependent on its basidiomycete fungus for food (Mueller *et al.* 2001) and the fungus requires dispersal via a special pouch of an *Atta* queen when she begins a new colony. When the ants of a colony die, the fungus is quickly overrun by bacteria and competing fungi, so the fates of fungus and ant are closely intertwined. Like the figs and fig wasps, they have partially congruent phylogenies (Mikheyev *et al.* 2006). Conflicts are likely to be low, though sex ratios could be contested because, like mitochondria, the fungus is maternally transmitted (Mueller 2002). Nevertheless, on our functional grounds, the interests of ants and fungi in a colony seem best viewed as organismally merged.

Indeed, one might add in the bacteria that live in specialized crypts in the ant's exoskeleton and protect the fungus (Currie *et al.* 2006). We by no means think that we should extend the concept of organismality further out to communities or to the biosphere in general (Lovelock 2000). But there are likely some highly cooperative multi-species assemblages with minimal conflict.

6. DISCUSSION

The 'major transitions' tradition (Buss 1982; Maynard Smith & Szathmáry 1995) has helped us to see that organisms could be prokaryotic groups of replicators, eukaryotic alliances with prokaryotic organelles, groups of cells and even societies. These steps have been critically important, but evolution does not work by major transitions alone. If evolution occasionally crafts new organismal alliances that are truly transformational, it seems likely that it will much more frequently craft new organismal alliances that are not necessarily revolutionary in the history of life, but organismal nevertheless. And if we want to understand the evolution of organismality, we should pay attention to the examples that are recent, to the ones that are unconventional and even to the ones that are incomplete. Our survey is a step in that direction, and it reveals a number of interesting points.

Control of conflict is viewed as one of the major prerequisites for a major transition. We agree that it is important, but low conflict and high cooperation are not the same thing; that is why we gave them separate axes in figures 1–3. Some groups have low conflict, but never become cooperative enough to be deemed organismal (clones of dandelions or non-social aphids, *Gonium*). Others have very high cooperation in spite of considerable conflict, with human societies being one familiar example. Organismality can evolve from either direction. *Volvox* and eusocial aphids evolved by adding cooperation in

simple groups lacking conflict, like *Gonium* or non-social aphids. Honeybees, in contrast, evolved by reducing conflicts in societies of more primitive bees.

Conflict can certainly be a threat to cooperation, but the two are not incompatible. High cooperation may even sometimes be what allows significant conflict. *Melipona* bees are in no danger of extinction despite their internecine battles, presumably because their colonies work so well in other ways. Vertebrates can sustain a huge amount of selfish junk DNA precisely because they are such successful cooperative entities in most respects.

Moreover, some conflict is not very disruptive to organismality (Travisano & Velicer 2004). The social amoeba *D. discoideum* has numerous cheater mutants that produce normal fruiting bodies on their own (Santorelli *et al.* 2008), so the spread of such cheaters would not destroy cooperation. This is one way in which our organism concept differs from a unit of selection; there can sometimes be considerable within-individual selection favouring such facultative cheaters without much damage to adaptation at a higher level.

Having defined organisms by what we consider to be their essential traits, high cooperation and very low conflict, we can now examine what is not essential to near conflict-free cooperation. Although most conventional organisms have a coherent body, contiguity is neither necessary nor sufficient for organismality. *Dictyostelium* and *Myxococcus* show that organisms can be assembled instead from formerly distinct parts.

We argue further that not only can organisms come together from separate entities, but they may also be organismal without attachment. Honeybees retain their independent bodies, but a growing consensus views them, and some other social insects, as superorganisms (Seeley 1989; Wilson & Sober 1989; Strassmann & Queller 2007; Hölldobler & Wilson 2008). Many microbial systems deserve similar consideration.

Social insects also show that clonality is not essential. In fact, relatedness is not required for organismality, as we know from the fusion of unrelated sperm and egg to form a new organism. Employing the same logic at a higher level, there seems to be no reason to exclude a hermaphroditic anglerfish that assembles from a separate male and female.

Indeed, we suggest that organismal aggregates do not even have to be of the same species. Again, conventional usage supports this, with the eukaryotic cell and some of its organelles providing the historical precedent. For consistency, we need to consider whether other mutualisms evolve to be organismal. Some, like aphid–*Buchnera*, seem fairly clear, particularly when there is vertical transmission to reduce conflicts. But vertical transmission does not seem necessary. Figs and their fig wasps have horizontal cotransmission (female wasp carries pollen). Though we need to probe more deeply for conflicts, it seems likely that organisms can even form using symbionts freshly acquired from the environment, as in the squid and its *Vibrio* bacteria or corals and the zooxanthellae.

An implication of the above is that the organism does not necessarily reside in a single lineage. Two branches of the evolutionary tree can fuse to form an

organism, and the two components may not speciate together. This may seem odd, but it is consistent with our view of a bacterium as a good organism, even though plasmids and even chunks of chromosomal genes hop between lineages at varying rates.

Though we are proposing a novel definition for organisms, there may be a place for multiple organism concepts, just as there are multiple species concepts (Wilson 1999; Pepper & Herron 2008). But it seems to us that the simplest way to include all conventionally accepted organisms is to define them in terms of extensive cooperation with little conflict. For consistency, this requires us to broaden our conception of organismality. This is more than a semantic game of deciding that X is an organism and Y is not. The scientific community could choose any name they want for entities with extensive cooperation and very little conflict, but the existence of such entities is one of the striking features of life, and explaining how they evolve should therefore be an important task. That task will be hamstrung if we restrict ourselves to those transitions that happened to have major consequences. Expanding our view beyond the major transitions suggests that there are multiple ways to achieve this degree of functional integration, and that many of the conditions that might be thought to be essential are not.

We thank the US National Science Foundation for support (EF-0328455, DEB-0816690). We thank Stuart West, Andy Gardner and Max Burton-Chellew for comments on the manuscript.

REFERENCES

- Adams, G. 1981 Search paths of fireflies in two dimensions. *Fla. Entomol.* **64**, 66–73. (doi:10.2307/3494601)
- Afkhami, M. & Rudgers, J. 2008 Symbiosis lost: imperfect vertical transmission of fungal endophytes in grasses. *Am. Nat.* **172**, 405–416. (doi:10.1086/589893)
- Anderson, R., Koella, J. & Hurd, H. 1999 The effect of *Plasmodium yoelii nigeriensis* infection on the feeding persistence of *Anopheles stephensi* Liston throughout the sporogonic cycle. *Proc. R. Soc. Lond. B* **266**, 1729–1733.
- Arnqvist, G. & Rowe, L. 2005 *Sexual conflict*. Princeton, NJ: Princeton University Press.
- Brandt, M., Foitzik, S., Fischer-Blass, B. & Heinze, J. 2005 The coevolutionary dynamics of obligate ant social parasite systems—between prudence and antagonism. *Biol. Rev.* **80**, 251–267. (doi:10.1017/S1464793104006669)
- Bronstein, J. 2001 The exploitation of mutualisms. *Ecol. Lett.* **4**, 277–287. (doi:10.1046/j.1461-0248.2001.00218.x)
- Bronstein, J., Alarcón, R. & Geber, M. 2006 The evolution of plant–insect mutualisms. *New Phytol.* **172**, 412–428. (doi:10.1111/j.1469-8137.2006.01864.x)
- Bshary, R. & Grutter, A. 2002 Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.* **63**, 547–555. (doi:10.1006/anbe.2001.1937)
- Bshary, R. & Schäffer, D. 2002 Choosy reef fish select cleaner fish that provide a high-quality service. *Anim. Behav.* **63**, 557–564. (doi:10.1006/anbe.2001.1923)
- Burger, J. & Gochfeld, M. 1982 Host selection as an adaptation to host-dependent foraging success in the cattle egret (*Bubulcus ibis*). *Behaviour* **79**, 212–229. (doi:10.1163/156853982X00265)
- Burt, A. & Trivers, R. 2006 *Genes in conflict: the biology of selfish genetic elements*. Cambridge, MA: Belknap.
- Buss, L. W. 1982 Somatic cell parasitism and the evolution of somatic tissue compatibility. *Proc. Natl Acad. Sci. USA* **79**, 5337–5341. (doi:10.1073/pnas.79.17.5337)
- Buss, L. W. 1987 *The evolution of individuality*. Princeton, NJ: Princeton University Press.
- Chapman, T. 2001 Seminal fluid-mediated fitness traits in *Drosophila*. *Heredity* **87**, 511–521. (doi:10.1046/j.1365-2540.2001.00961.x)
- Charlat, S., Hurst, G. & Merçot, H. 2003 Evolutionary consequences of *Wolbachia* infections. *Trends Genet.* **19**, 217–223. (doi:10.1016/S0168-9525(03)00024-6)
- Clay, K., Holah, J. & Rudgers, J. 2005 Herbivores cause a rapid increase in hereditary symbiosis and alter plant community composition. *Proc. Natl Acad. Sci. USA* **102**, 12 465–12 470. (doi:10.1073/pnas.0503059102)
- Crespi, B. J. 2001 The evolution of social behaviour in microorganisms. *Trends Ecol. Evol.* **16**, 178–183. (doi:10.1016/S0169-5347(01)02115-2)
- Currie, C. R., Poulsen, M., Mendenhall, J., Boomsma, J. J. & Billen, J. 2006 Coevolved crypts and exocrine glands support mutualistic bacteria in fungus-growing ants. *Science* **311**, 81–85. (doi:10.1126/science.1119744)
- Davidson, E., Peterson, K. & Cameron, R. A. 1995 Origin of bilaterian body plans: evolution of developmental regulatory mechanisms. *Science* **270**, 1319–1325. (doi:10.1126/science.270.5240.1319)
- Dawkins, R. 1982 *The extended phenotype*. Oxford, UK: W. H. Freeman.
- Douglas, A. 2008 Conflict, cheats and the persistence of symbioses. *New Phytol.* **177**, 849–858. (doi:10.1111/j.1469-8137.2007.02326.x)
- Downhower, J. F. & Wilson, D. E. 1973 Wasps as a defense mechanism of katydids. *Am. Midl. Nat.* **89**, 451–455. (doi:10.2307/2424050)
- Dufaÿ, M. & Anstett, C. 2003 Conflicts between plants and pollinators that reproduce within inflorescences: evolutionary variations on a theme. *Oikos* **100**, 3–14. (doi:10.1034/j.1600-0706.2003.12053.x)
- Engels, W. & Imperatriz-Fonseca, V. L. 1990 Caste development, reproductive strategies and control of fertility in honey bees and stingless bees. In *Social insects: an evolutionary approach to castes and reproduction* (ed. W. Engels), pp. 166–230. Berlin, Germany: Springer-Verlag.
- Ennis, H. L., Dao, D. N., Pukatzi, S. U. & Kessin, R. H. 2000 *Dictyostelium* amoebae lacking an F-box protein form spores rather than stalk in chimeras with wild type. *Proc. Natl Acad. Sci. USA* **97**, 3292–3297. (doi:10.1073/pnas.050005097)
- Fleming, T. & Holland, J. 1998 The evolution of obligate pollination mutualisms: senita cactus and senita moth. *Oecologia* **114**, 368–375. (doi:10.1007/s004420050459)
- Fogarty, M. & Hetrick, W. 1973 Summer foods of cattle egrets in North Central Florida. *Auk* **90**, 268–280.
- Foster, K. In press. Social behaviour in microorganisms. In *Social behaviour: genes, ecology and evolution* (eds T. Szekely, A. Moore & J. Komdeur). Cambridge, UK: Cambridge University Press.
- Foster, K. & Kokko, H. 2006 Cheating can stabilize cooperation in mutualisms. *Proc. R. Soc. B* **273**, 2233–2239. (doi:10.1098/rspb.2006.3571)
- Frank, S. 1989 The evolutionary dynamics of cytoplasmic male sterility. *Am. Nat.* **133**, 345–376. (doi:10.1086/284923)
- Frank, S. 1996 Host control of symbiont transmission: the separation of symbionts into germ and soma. *Am. Nat.* **148**, 1113–1124.
- Frank, S. A. & Nowak, M. A. 2004 Problems of somatic mutation and cancer. *BioEssays* **26**, 291–299. (doi:10.1002/bies.20000)

- Gardner, A. & Grafen, A. 2009 Capturing the superorganism: a formal theory of group adaptation. *J. Evol. Biol.* **22**, 659–671. (doi:10.1111/j.1420-9101.2008.01681.x)
- Gilbert, O. M., Foster, K. R., Mehdiabadi, N. J., Strassmann, J. E. & Queller, D. C. 2007 High relatedness maintains multicellular cooperation in a social amoeba by controlling cheater mutants. *Proc. Natl Acad. Sci. USA* **104**, 8913–8917. (doi:10.1073/pnas.0702723104)
- Gore, J., Hyuk, H. & van Oudenaarden, A. 2009 Snowdrift game dynamics and facultative cheating in yeast. *Nature* **459**, 253–256. (doi:10.1038/nature07921)
- Greig, D. & Travisano, M. 2004 The prisoner's dilemma and polymorphism in yeast SUC genes. *Proc. R. Soc. Lond. B* **271**, S25–S26. (doi:10.1098/rsbl.2003.0083)
- Haig, D. 2000 The kinship theory of genomic imprinting. *Ann. Rev. Ecol. Syst.* **31**, 9–32. (doi:10.1146/annurev.ecolsys.31.1.9)
- Herre, E. 1989 Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps. *Experientia* **45**, 637–647.
- Herre, E., Knowlton, N., Mueller, U. & Rehner, S. 1999 The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol. Evol.* **14**, 49–53. (doi:10.1016/S0169-5347(98)01529-8)
- Herre, E., Jandér, K. & Machado, C. 2008 Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annu. Rev. Ecol. Syst.* **39**, 439–458. (doi:10.1146/annurev.ecolsys.37.091305.110232)
- Herron, M. & Michod, R. 2008 Evolution of complexity in the volvocine algae: transitions in individuality through darwin's eye. *Evolution* **62**, 436–451. (doi:10.1111/j.1558-5646.2007.00304.x)
- Hölldobler, B. & Wilson, E. 2008 *The superorganism: the beauty, elegance, and strangeness of insect societies*. New York, NY: W. W. Norton.
- Honegger, R. 1998 The lichen symbiosis—what is so spectacular about it? *Lichenologist* **30**, 193–212.
- Hull, D. 1980 Individuality and selection. *Ann. Rev. Ecol. Syst.* **11**, 311–332. (doi:10.1146/annurev.es.11.110180.001523)
- Hurst, L. D. 1998 Selfish genes and meiotic drive. *Nature* **391**, 223. (doi:10.1038/34523)
- Hurst, G. & Werren, J. 2001 The role of selfish genetic elements in eukaryotic evolution. *Nat. Rev. Genet.* **2**, 597–606. (doi:10.1038/35084545)
- Hyvärinen, M., Härdling, R. & Tuomi, J. 2002 Cyanobacterial lichen symbiosis: the fungal partner as an optimal harvester. *Oikos* **98**, 498–504. (doi:10.1034/j.1600-0706.2002.980314.x)
- Johnson, S. & Steiner, K. 2000 Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* **15**, 140–143. (doi:10.1016/S0169-5347(99)01811-X)
- Jouventin, P., Charmantier, A., Dubois, M.-P., Jarne, P. & Bried, J. 2007 Extra-pair paternity in the strongly monogamous wandering albatross *Diomedea exulans* has no apparent benefits for females. *Ibis* **149**, 67–78.
- Kerr, B., Riley, M. A., Feldman, M. W. & Bohannan, B. J. M. 2002 Local dispersal promotes biodiversity in a real-life game of rock–scissors–paper. *Nature* **418**, 171–174. (doi:10.1038/nature00823)
- Kiers, E. & Denison, R. 2008 Sanctions, cooperation, and the stability of plant–rhizosphere mutualisms. *Annu. Rev. Ecol. Syst.* **39**, 315–236.
- Koella, J. C., Sørensen, F. L. & Anderson, R. A. 1998 The malaria parasite, *Plasmodium falciparum*, increases the frequency of multiple feeding of its mosquito vector *Anopheles gambiae*. *Proc. R. Soc. Lond. B* **265**, 763–768.
- Koonin, E. & Martin, W. 2005 On the origin of genomes and cells within inorganic compartments. *Trends Genet.* **21**, 647–654. (doi:10.1016/j.tig.2005.09.006)
- Krüger, O. 2007 Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. *Phil. Trans. R. Soc. B* **362**, 1873–1886. (doi:10.1098/rstb.2006.1849)
- Lander, E. *et al.* 2001 Initial sequencing and analysis of the human genome. *Nature* **409**, 860–921. (doi:10.1038/35057062)
- Lefèvre, T., Koella, J., Renaud, F., Hurd, H., Biron, D. & Thomas, T. 2006 New prospects for research on manipulation of insect vectors by pathogens. *PLoS Pathog.* **2**, e72. (doi:10.1371/journal.ppat.0020072)
- Lovelock, J. 2000 *Gaia: A new look at life on earth*. Oxford, UK: Oxford University Press.
- Lutzoni, F., Pagel, M. & Reeb, V. 2001 Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* **411**, 937–940. (doi:10.1038/35082053)
- Lyttle, T. 1991 Segregation distorters. *Annu. Rev. Genet.* **25**, 511–557. (doi:10.1146/annurev.ge.25.120191.002455)
- Margulis, L. 1970 *Origin of eukaryotic cells*. New Haven, CT: Yale University Press.
- Maynard Smith, J. & Szathmáry, E. 1995 *The major transitions in evolution*. Oxford, UK: W. H. Freeman.
- McCallum, H. & Jones, M. 2006 To lose both would look like carelessness: Tasmanian devil facial tumour disease. *PLoS Biol.* **4**, 1671–1674.
- Mehdiabadi, N. J. *et al.* 2006 Kin preference in a social microorganism. *Nature* **442**, 881–882. (doi:10.1038/442881a)
- Michod, R. 2000 *Darwinian dynamics: evolutionary transitions in fitness and individuality*. Princeton, NJ: Princeton University Press.
- Michod, R. E. & Roze, D. 1999 Cooperation and conflict in the evolution of multicellularity. *Heredity* **86**, 1–7. (doi:10.1046/j.1365-2540.2001.00808.x)
- Mikheyev, A., Mueller, U. & Abbot, P. 2006 Cryptic sex and many-to-one coevolution in the fungus-growing ant symbiosis. *Proc. Natl Acad. Sci. USA* **103**, 10 702–10 706. (doi:10.1073/pnas.0601441103)
- Møller, A. 2002 Sexual selection in the barn swallow. In *Model systems in behavioural ecology: integrating conceptual, theoretical, and empirical approaches* (ed. L. Dugatkin), pp. 359–377. Princeton, NJ: Princeton University Press.
- Moore, J. 2002 *Parasites and the behaviour of animals*. Oxford, UK: Oxford University Press.
- Moran, N. 2007 Symbiosis as an adaptive process and source of phenotypic complexity. *Proc. Natl Acad. Sci. USA* **104**, 8627–8633. (doi:10.1073/pnas.0611659104)
- Mueller, U. 2002 Ant versus fungus versus mutualism: ant-cultivar conflict and the deconstruction of the attine ant–fungus symbiosis. *Am. Nat.* **160**, S67–S98. (doi:10.1086/342084)
- Mueller, U., Schultz, T., Currie, C., Adams, R. & Malloch, D. 2001 The origin of the attine ant–fungus mutualism. *Q. Rev. Biol.* **76**, 169–197. (doi:10.1086/393867)
- Nelson, M. & Gargas, A. 2007 Dissociation and horizontal transmission of codispersing lichen symbionts in the genus *Lepraria* (Lecanorales: Stereocaulaceae). *New Phytol.* **177**, 264–275.
- Nyholm, S. & McFall-Ngai, M. 2004 The winnowing: establishing the squid–*Vibrio* symbiosis. *Nat. Rev. Microbiol.* **2**, 632–643. (doi:10.1038/nrmicro957)
- Ostrowski, E. 2008 Kin discrimination increases with genetic distance in a social amoeba. *PLoS Biol.* **6**, 2376–2382.

- Pellmyr, O., Thompson, J., Brown, J. & Harrison, R. 1996 Evolution of pollination and mutualism in the yucca moth lineage. *Am. Nat.* **148**, 827–847. (doi:10.1086/285958)
- Pepper, J. & Herron, M. 2008 Does biology need an organism concept? *Biol. Rev.* **83**, 621–627.
- Peters, J. M., Queller, D. C., Imperatriz-Fonseca, V. L., Roubik, D. W. & Strassmann, J. E. 1999 Mate number, kin selection and social conflicts in stingless bees and honey bees. *Proc. R. Soc. Lond. B* **266**, 379–384. (doi:10.1098/rspb.1999.0648)
- Piercey-Normore, M. & DePriest, P. 2001 Algal switching among lichen symbioses. *Am. J. Bot.* **88**, 1490–1498. (doi:10.2307/3558457)
- Pietsch, T. 2005 Dimorphism, parasitism, and sex revisited: modes of reproduction among deep-sea ceratoid anglerfishes (Teleostei: Lophiiformes). *Ichthy. Res.* **52**, 207–236. (doi:10.1007/s10228-005-0286-2)
- Pineda-Krch, M. & Lehtila, K. 2004 Costs and benefits of genetic heterogeneity within organisms. *J. Evol. Biol.* **17**, 1167–1177.
- Queller, D. 1997 Cooperators since life began. Book review of: The major transitions in evolution, by J. Maynard Smith and E. Szathmari. *Q. Rev. Biol.* **72**, 184–188. (doi:10.1086/419766)
- Queller, D. C. 2003 Theory of genomic imprinting conflict in social insects. *BMC Evol. Biol.* **3**, 15. (doi:10.1186/1471-2148-3-15)
- Queller, D. C., Foster, K. R., Fortunato, A. & Strassmann, J. E. 2003 Cooperation and conflict in the social amoeba, *Dictyostelium discoideum*. In *Social insects and sociogenetics* (eds T. Kikuchi, T. Kubo & S. Higashi), pp. 173–200. Sapporo, Japan: Hokkaido University Press.
- Ratnieks, F. L. W. & Visscher, P. K. 1989 Worker policing in the honeybee. *Nature* **342**, 796–797. (doi:10.1038/342796a0)
- Ratnieks, F., Foster, K. R. & Wenseleers, T. 2006 Conflict resolution in insect societies. *Annu. Rev. Entomol.* **51**, 581–608. (doi:10.1146/annurev.ento.51.110104.151003)
- Razakandrainibe, F. G., Durand, P., Koella, J. C., De Meeüs, T., Rousset, F., Ayala, F. J. & Renaud, F. 2005 'Clonal' population structure of the malaria agent *Plasmodium falciparum* in high-infection regions. *Proc. Natl Acad. Sci. USA* **102**, 17 388–17 393. (doi:10.1073/pnas.0508871102)
- Reisner, A., Höller, B., Molin, S. & Zechner, E. 2006 Synergistic effects in mixed *Escherichia coli* biofilms: conjugative plasmid transfer drives biofilm expansion. *J. Bacteriol.* **188**, 3582–3588. (doi:10.1128/JB.188.10.3582-3588.2006)
- Rønsted, N., Weiblen, G., Clement, W., Zerega, N. & Savolainen, V. 2006 Reconstructing the phylogeny of figs (*Ficus*, Moraceae) to reveal the history of fig pollination mutualism. *Symbiosis* **45**, 45–56.
- Ross, C., French, J. A. & Orti, G. 2007 Germ-line chimerism and paternal care in marmosets (*Callithrix kuhlii*). *Proc. Natl Acad. Sci. USA* **104**, 6278–6282. (doi:10.1073/pnas.0607426104)
- Sachs, J. & Simms, E. 2008 The origins of uncooperative bacteria. *Oikos* **117**, 961–966. (doi:10.1111/j.0030-1299.2008.16606.x)
- Sachs, J. L., Mueller, U. G., Wilcox, T. P. & Bull, J. J. 2004 The evolution of cooperation. *Q. Rev. Biol.* **79**, 135–160. (doi:10.1086/383541)
- Sanders, W. 2006 A feeling for the superorganism: expression of plant form in the lichen thallus. *Bot. J. Linn. Soc.* **150**, 89–99. (doi:10.1111/j.1095-8339.2006.00497.x)
- Santelices, B. 1999 How many kinds of individual are there? *Trends Ecol. Evol.* **14**, 152–155. (doi:10.1016/S0169-5347(98)01519-5)
- Santorelli, L. *et al.* 2008 Facultative cheater mutants reveal the genetic complexity of cooperation in social amoebae. *Nature* **451**, 1107–1110. (doi:10.1038/nature06558)
- Sapp, J. 2004 The dynamics of symbiosis: an historical overview. *Can. J. Bot.* **82**, 1046–1056. (doi:10.1139/b04-055)
- Seeley, T. D. 1989 The honey bee colony as a superorganism. *Am. Sci.* **77**, 546–553.
- Shaulsky, G. & Kessin, R. 2003 The cold war of the social amoebae. *Curr. Biol.* **17**, R684–R692. (doi:10.1016/j.cub.2007.06.024)
- Silvieus, S., Clement, W. & Weiblen, G. 2007 Cophylogeny of figs, pollinators, gallers, and parasitoids. In *Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects* (ed. K. Tilmon), pp. 225–239. Berkeley, CA: University of California Press.
- Smith, J. 2001 The social evolution of bacterial pathogenesis. *Proc. R. Soc. Lond. B* **268**, 61–69. (doi:10.1098/rspb.2000.1330)
- Smukalla, S. *et al.* 2008 *FLO1* is a variable green beard gene that drives biofilm-like cooperation in budding yeast. *Cell* **135**, 726–737. (doi:10.1016/j.cell.2008.09.037)
- Strassmann, J. & Queller, D. 2007 Insect societies as divided organisms: the complexities of purpose and cross-purpose. *Proc. Natl Acad. Sci. USA* **104**, 8619–8626. (doi:10.1073/pnas.0701285104)
- Stutt, A. D. & Siva-Jothy, M. T. 2001 Traumatic insemination and sexual conflict in the bed bug *Cimex lectularius*. *Proc. Natl Acad. Sci. USA* **98**, 5683–5687. (doi:10.1073/pnas.101440698)
- Thomas, F., Adamo, S. & Moore, J. 2004 Parasitic manipulation: where are we and where should we go? *Behav. Proc.* **68**, 185–189. (doi:10.1016/j.beproc.2004.06.010)
- Tóth, E., Queller, D. C., Dollin, A. & Strassmann, J. E. 2004 Conflict over male parentage in stingless bees. *Insect Soc.* **51**, 1–11. (doi:10.1007/s00040-003-0707-z)
- Travisano, M. & Velicer, G. J. 2004 Strategies of microbial cheater control. *Trends Microbiol.* **12**, 72–78. (doi:10.1016/j.tim.2003.12.009)
- Turner, P. E. & Chao, L. 1999 Prisoner's Dilemma in an RNA virus. *Nature* **398**, 441–443. (doi:10.1038/18913)
- Velicer, G. J. 2003 Social strife in the microbial world. *Trends Microbiol.* **11**, 330–337. (doi:10.1016/S0966-842X(03)00152-5)
- Velicer, G. & Stredwick, K. 2002 Experimental social evolution with *Myxococcus xanthus*. *Antonie Van Leeuwenhoek* **81**, 155–164. (doi:10.1023/A:1020546130033)
- Velicer, G. J., Kroos, L. & Lenski, R. E. 1998 Loss of social behaviours by *Myxococcus xanthus* during evolution in an unstructured habitat. *Proc. Natl Acad. Sci. USA* **95**, 12 376–12 380. (doi:10.1073/pnas.95.21.12376)
- Velicer, G. J., Kroos, L. & Lenski, R. E. 2000 Developmental cheating in the social bacterium *Myxococcus xanthus*. *Nature* **404**, 598–601. (doi:10.1038/35007066)
- Visick, K. & McFall-Ngai, M. 2000 An exclusive contract: specificity in the *Vibrio fischeri*–*Euprymna scolopes* partnership. *J. Bacteriol.* **182**, 1779–1787. (doi:10.1128/JB.182.7.1779-1787.2000)
- Visick, K. & Ruby, E. 2006 *Vibrio fischeri* and its host: it takes two to tango. *Curr. Opin. Microbiol.* **9**, 1–7.
- Weeks, P. 2000 Red-billed oxpeckers: vampires or tickbirds? *Behav. Ecol.* **11**, 154–160. (doi:10.1093/beheco/11.2.154)
- Wenseleers, T. & Ratnieks, F. L. W. 2004 Tragedy of the commons in *Melipona* bees. *Proc. R. Soc. Lond. B* **271**, S310–S312. (doi:10.1098/rsbl.2003.0159)
- Wernegreen, J. & Moran, N. 2001 Vertical transmission of biosynthetic plasmids in aphid endosymbionts (*Buchnera*). *J. Bacteriol.* **183**, 785–790. (doi:10.1128/JB.183.2.785-790.2001)

- West, S. A., Griffin, A. S., Gardner, A. & Diggle, S. P. 2006 Social evolution theory for microorganisms. *Nat. Rev. Microbiol.* **4**. (doi:10.1038/nrmicro1461)
- Wheeler, W. M. 1911 The ant colony as organism. *J. Morph.* **22**, 307–325. (doi:10.1002/jmor.1050220206)
- Wilson, J. 1999 *Biological individuality: the identity and persistence of living entities*. Cambridge, UK: Cambridge University Press.
- Wilson, J. 2000 Ontological butchery: organism concepts and biological generalizations. *Phil. Sci.* **67**, S301–S311. (doi:10.1086/392827)
- Wilson, D. S. & Sober, E. 1989 Reviving the superorganism. *J. Theor. Biol.* **136**, 337–356. (doi:10.1016/S0022-5193(89)80169-9)
- Wireman, J. & Dworkin, M. 1977 Developmentally induced autolysis during fruiting body formation by *Myxococcus xanthus*. *J. Bacteriol.* **129**, 798–802.
- Woese, C. & Olsen, G. 1986 Archaeobacterial phylogeny: perspectives on the urkingdoms. *Syst. Appl. Microbiol.* **7**, 161–177.
- Xavier, J. & Foster, K. 2007 Cooperation and conflict in microbial biofilms. *Proc. Natl Acad. Sci. USA* **104**, 876–881. (doi:10.1073/pnas.0607651104)
- Yu, D., Ridley, J., Jouselin, E., Herre, E., Compton, S., Cook, J., Moore, J. & Weiblen, G. 2004 Oviposition strategies, host coercion and the stable exploitation of figs by wasps. *Proc. R. Soc. Lond. B* **271**, 1185–1195. (doi:10.1098/rspb.2003.2630)
- Yuan, X., Xiao, S. & Taylor, T. 2005 Lichen-like symbiosis 600 million years ago. *Science* **308**, 1017–1020. (doi:10.1126/science.1111347)
- Zoller, S. & Lutzoni, F. 2003 Slow algae, fast fungi: exceptionally high nucleotide substitution rate differences between lichenized fungi *Omphalina* and their symbiotic green algae *Coccomyxa*. *Mol. Phylogenet. Evol.* **29**, 629–640. (doi:10.1016/S1055-7903(03)00215-X)