

THE SOCIAL ORGANISM: CONGRESSES, PARTIES, AND COMMITTEES

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We propose that what makes an organism is nearly complete cooperation, with strong control of intraorganism conflicts, and no affiliations above the level of the organism as unified as those at the organism level. Organisms can be made up of like units, which we call fraternal organisms, or different units, making them egalitarian organisms. Previous definitions have concentrated on the factors that favor high cooperation and low conflict, or on the adapted outcomes of organismality. Our approach brings these definitions together, conceptually unifying our understanding of organismality. Although the organism is a concerted cluster of adaptations, nearly all directed toward the same end, some conflict may remain. To understand such conflict, we extend Leigh's metaphor of the parliament of genes to include parties with different interests and committees that work on particular tasks.

KEY WORDS: Individuality, major transitions, multicellularity, organism, symbiosis, superorganism.

What Are Organisms?

Why have so many living entities united into complex, adapted units from much simpler entities? Why does the ocean have blue whales, giant kelp, and corals in addition to the viruses and bacteria that inhabit every drop of water by the millions? What are the essential features of these units we call organisms? This question was much debated in the 19th and early 20th centuries, with much agreement on some central issues, but considerable disagreement around the fringes (Huxley 1912). The debate could be viewed as a sterile matter of mere definitional preferences, but a good definition points to important ideas and to important questions (Table 1).

In this spirit, we proposed in a previous paper that what makes an organism is high and near-unanimous cooperation among its constituent parts, with actual conflicts among those parts largely absent or controlled (Queller and Strassmann 2009). This is a view of organisms as cooperative social groups and it thus links the concept to one of the most significant evolutionary questions of the last 50 years, the evolution of cooperation. Since at least 1971, when Leigh described organisms as parliaments of genes (Leigh 1971), it has been recognized that organisms are analogous

in some sense to social groups with potentially different interests. Later work on the major evolutionary transitions (Buss 1987; Maynard Smith and Szathmáry 1995) made it clear that organisms actually consist of several different levels of groups. Independent replicators came together into prokaryotic cells. Several prokaryotic cells joined to make a eukaryotic cell. Cells cooperate to form multicellular organisms. And we shall argue, as have others, that some groups of multicellular organisms have become organismal. Genes may be selfish, but they nearly always seem to operate in cooperative alliances.

Besides linking to an important question, this definition centers on perhaps the key distinguishing feature of living things: adaptation. High cooperation and low conflict is another way of saying that the organism is the focus of adaptation. There may be adaptations both below and above the level of the organism, but it is a biological reality that most adaptations occur in discrete bundles, and that within each bundle nearly all adaptations function toward a common end. These bundles of adaptations are what we call organisms.

Conflict and cooperation are often viewed on a single axis, because the same factors are expected to affect both. However, we consider conflict separately from cooperation because in the real

Table 1. A sampling of quotes defining individuals and organisms.

Quote	Reference
The individual animal is the sum of the phenomena presented by a single life: in other words, it is, all those forms which proceed from a single egg, taken together.	Huxley 1852, pp. 187–188
as in animals (at least in their higher orders,) it appears clear and simple . . . Among the higher animals, the individual appears as a member of a race produced by sexual generation; and this very test may be applied to plants, except in the very lowest forms.	Braun 1853 (translated by Stone), p. 300
An organism is a complex, definitely coordinated and therefore individualized system of activities, which are primarily directed to obtaining and assimilating substances from an environment, to producing other similar systems, known as offspring, and to protecting the system itself and usually also its offspring from disturbances emanating from the environment.	Wheeler 1911, p. 308
. . . the individual must have heterogeneous parts, whose function only gains full significance when considered in relation to the whole; it must have some independence of the forces of inorganic nature; and it must work, and work after such a fashion that it, or a new individual formed from part of its substance, continues able to work in a similar way.	Huxley 1912, p. 28
[considering animals only] First, their existence as definite bodies marked off in space and separate from other bodies . . . ; secondly their power of movement; and thirdly their growth . . .	Huxley 1912, p. 50
[on lichens] The fungus gains more than the alga, but this does not prevent the combination of both, the lichen, from being a very definite individual. A lichen on a barren rock is something whose continuance as such and in such a situation is dependent on the cooperation of its two constituents.	Huxley 1912, p. 124
[on yucca and yucca moth] The Yucca and its moth, for instance, constitute a definite individual that works for its own perpetuation.	Huxley 1912, p. 142
[social insects] The communities of ants and bees are undoubted individuals.	Huxley 1912, p. 142
In short, the organic individual appears to be a unity of some sort, its individuality consists largely of this unity and the process of individuation is the process of integration of a mere aggregation into such a unity . . .	Child 1915, pp. 2–3
The organism is a harmonious whole in which not only the organ functions are adapted to one another, but in which all the various tissues, which apparently are not functionally related, are specifically adapted to each other. [i.e., no transplantation rejection]	Loeb 1937, p. 5
Individuality . . . life became fragmented into physiologically isolated individuals and genetically separate lines of descent.	Williams 1966, p. 136
. . . organisms . . . as life cycles . . .	Bonner 1974, p. 11
. . . the “individual” of evolutionary biology. The latter individual has “reproductive fitness” and is the unit of selection in most evolutionary conceptualizations. [counts dandelion clones and aphid clones as individuals]	Janzen 1977, p. 586
Organism: any living creature	Wilson 1975, p. 590
Individuals are spatiotemporally localized entities that have reasonably sharp beginnings and endings in time.	Hull 1980, p. 313
An organism is the physical unit associated with one single life cycle . . . The organism has the following attributes. It is either a single cell, or if it is multicellular its cells are close genetic kin of each other: they are descended from a single stem cell, which means that they have a more recent common ancestor with each other than with any other cells of any other organism.	Dawkins 1982 pp. 259, 263
. . . by “organism” I mean an entire life cycle.	Donoghue 1985, p. 177
We tend to call a biological object an organism if it maintains no permanent physical connection with others and if its parts are so well integrated that they work only in coordination and for the proper function of the whole.	Gould 1985, p. 93
An individual is a physiologically discrete organism.	Buss 1987, p. viii
Individuals can be regarded as groups of genes that have become functionally organized by natural selection to perpetuate themselves.	Wilson and Sober 1989, p. 341

Continued.

Table 1. Continued.

Quote	Reference
We designate something as an organism, not because it is <i>n</i> steps up on the ladder of life, but because it is a consolidated unit of design, the focal point where lines of adaptation converge. It is where history has conspired to make between-unit selection efficacious and within-unit selection impotent.	Queller 1997, p. 187
[Not all need apply.] 1. An individual is a particular. 2. It is a historical entity. 3. It is a functional individual. 4. It is a genetic individual. 5. It is a developmental individual. 6. It is a unit of evolution.	Wilson 1999, p. 60
The three attributes of individuality (genetic uniqueness, genetic homogeneity, and autonomy) are conceived as axes with minimal possible variability . . .	Santelices 1999, p. 153
. . . an organism is: a. a living agent b. that belongs to a reproductive lineage, some of whose members have the potential to possess an intergenerational life cycle, and c. which has minimal functional autonomy.	Wilson 2005, p. 59
. . . the “organism syndrome” results from positive feedback between natural selection and functional integration.	Pepper and Herron 2008, p. 626
Organism: An individual living system, such as an animal, plant, or microorganism, that is capable of reproduction, growth, and maintenance.	Dictionary of Biology, Oxford University Press, 2008
In biology, an organism is any living system (such as animal, plant, fungus, or microorganism). In at least some form, all organisms are capable of response to stimuli, reproduction, growth and development, and maintenance of homeostasis as a stable whole.	Wikipedia, 5 Sept. 2009
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.	Queller and Strassmann 2009

world they do not covary perfectly. There are highly cooperative groups that also have very high levels of conflict. Under these circumstances, the adaptations work at cross-purposes. Likewise, there can be groups entirely lacking in conflict that are not particularly cooperative. In this case there is little or no adaptation at the group level. Therefore, conflict and cooperation can be viewed as separate orthogonal axes, with the space of highest cooperation

and lowest conflict constituting organismality (Fig. 1). Quadrants with high cooperation and high conflict we call societies; low cooperation and low conflict are simple groups; low cooperation and low conflict are competitors (Queller and Strassmann 2009). The dividing lines between these entities are arbitrary at some level, but restricting organisms to nearly unanimous cooperation and low conflict gives a stringent and clear definition

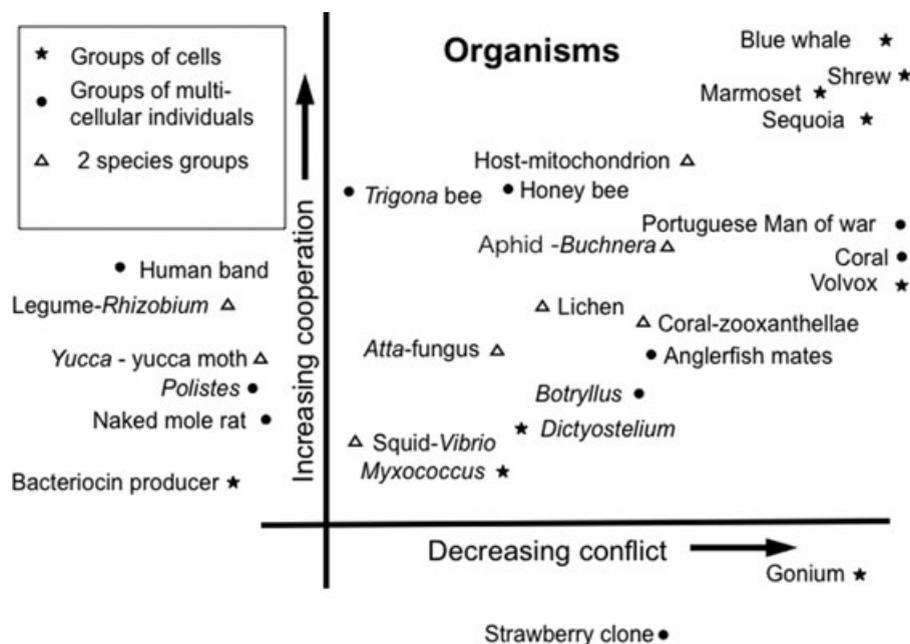


Figure 1. Examples of organisms and their levels of cooperation and conflict.

of organismality. Exactly where any given organism falls in the space on Figure 1 represents our best estimate of characteristics that are not always easy to quantify.

It is actual conflict and actual cooperation and not the theoretical possibility of conflict or cooperation that is important for defining organismality. Potential or theoretical conflict or cooperation, as defined for example by genetic similarity, may or may not be actualized. Real entities, like organisms, ought to be defined in real terms and only then explained by theoretical concepts such as potential conflict and cooperation. We therefore place no other preconditions on what we call an organism. We should consider all levels of organization: organisms could be single-celled, multicelled, colonial, or symbiotic so long as they are made up of highly cooperative members with low actual conflict. We are open-minded about other issues like genetic homogeneity and physical contiguity. Below we develop this idea, describe some organisms according to this scheme, discuss how organismality can be achieved, and extend the metaphor of parliaments to organisms.

Our approach points to two important questions. The first is what entities qualify as organisms—how many groups have evolved an extreme degree of cooperation that is nearly conflict-free? The second deals with how organisms evolve and particularly how they deal with conflict.

A fundamental distinction is whether members are similar kinds of units or different kinds. Queller (Queller 1997) has called these two kinds of collaborations fraternal and egalitarian after two prongs of the French revolutionary slogan (the third, libertarians, are nonsocial). They correspond to groupings due primarily to kin selection or to mutualism. Fraternal organisms comprised of like units include multicellular organisms and those made up of multiple individuals of the same species. They are held together by kinship and some units may therefore sacrifice themselves for others who will transmit the same genes. Egalitarian organisms, by contrast, are comprised of dissimilar units and include the bacterial cell, the eukaryotic cell, and some other symbioses. They are held together by complementary specializations, but this cannot extend to reproductive specialization because one partner cannot reproduce the others. Fraternal and egalitarian can refer to groupings at any level and organisms may consist of groupings at several levels; an elephant is a fraternal grouping of egalitarian eukaryotic cells.

FRATERNAL ORGANISMS

Groups of cells that have gone through a single-cell bottleneck and remain together are the paradigm organisms, readily recognized as such. Cats, dogs, lizards, and butterflies are examples of paradigm organisms. Because these organisms are clonal, they score lowest on the conflict scale, with each constituent member of the organism genetically identical to every other constituent member. Perhaps the most identical of clonal groups are those

that are the fewest cell divisions away from a single-celled progenitor, so a young shrew is usually more perfectly clonal than is an old blue whale, although these differences are likely to be very minor. This means that a blue whale would be slightly to the left, more conflict side of conflict as compared to the shrew (Fig 1).

These organisms also score very high on the cooperation scale because they form a physiologically cohesive single organism in which all constituent cells cooperate for the reproduction of the germ cells. One might say that cooperation increases with specialization, so that a larger individual with more cell types exhibits higher levels of cooperation than a smaller individual with fewer cell types (Bell and Mooers 1997).

Even within a multicellular organism, it is possible that selfish mutations can arise that cause some cell types to proliferate against the interests of the whole organism. These sorts of mutations are usually somatic cancers that may have a short-term cell replication advantage, but do not get passed on. Even when cells with replicative advantages can be passed on, it is difficult for them to spread because the single-cell bottleneck that initiates each new organism eliminates past within-organism variation (Queller 2000). Other conflicts can occur at a lower level, not among cells but among genes. These include meiotic drive, transposable elements, and genomic imprinting (Haig 2000; Burt and Trivers 2006). No one views these conflicts as sufficiently disruptive to negate organismality because the effects are usually minor, temporary, or well controlled. But their existence in the most paradigmatic of organisms is important because it means that we cannot hold other organisms to the impossible standard of having no conflicts at all.

There are likely to be multicellular organisms that do not go through a single-cell bottleneck. A good example is the social amoeba *Dictyostelium discoideum*, which is a solitary cell for most of its existence (Raper 1984). It moves through the soil with pseudopods, engulfs bacteria for food, and periodically divides by mitosis. Starvation triggers a transition. If there are sufficient amoebae in the area, they aggregate and then form a multicellular slug that crawls along toward light and heat, and away from ammonia, and ultimately forms a fruiting body in which about 20% of cells die to form a strong stalk which lifts the remaining cells above the substrate a millimeter or so (Bonner 1944). There they form hardy spores and await dispersal. The multicellular stage has organismal levels of cooperation but also potentially more conflict than a clonal organism. The aggregative origin of multicellularity in *Dictyostelium* makes it vulnerable to exploitation by selfish clones that produce spore cells and not stalk cells, (Strassmann et al. 2000; Santorelli et al. 2008), but if such conflicts prove to be sufficiently minor or rare—if actual conflict is low—there is every reason to view these aggregations as organismal.

Sociality is proving to be very common in microbes (Crespi 2001; West et al. 2006; Foster in press), and many other groups of

microbes may prove to be essentially organismal. Usually these would be in tight groups, for example biofilms (Nadell et al. 2007). A particularly intriguing possibility is that some cooperative pathogenic microbes (Griffin et al. 2004) might function as dispersed organisms, bounded and connected by the body of their host (Queller and Strassmann 2009).

There are also many fraternal associations of multicellular individuals. These have usually been classified as colonies rather than higher order organisms, but given that we know that organismality has previously taken jumps from one level to the next, we should consider which ones might have the combination of high cooperation and low conflict to qualify (Fig. 1). Much discussed in this respect are the Cnidarian siphonophores, such as the Portuguese Man of War. Instead of hundreds of kinds of cells, this organism is made up of four different kinds of multicellular individuals so specialized that they cannot live separately (Dunn and Wagner 2006). If one takes a narrow morphological view of organismality, these are mere colonies of organisms. Low conflict is the natural result of their clonality and cooperation is high, so by our definition they are definitely organismal. We think they are so unified that they would probably never have been called separate individuals but for their noncolonial relatives.

Other clonal groups may also qualify and we do not exclude a priori groups that remain unattached. Clonal social aphids that live in galls have differentiated sterile soldiers (Stern and Foster 1996). These aphid groups arguably have organismal levels of cooperation, although at levels lower than many other organisms, and they have an absence of conflict if there is no between-gall exchange (Abbot et al. 2001).

However, the best examples of dispersed cooperative groups with minimal conflict are not clonal. Many social ants, bees, wasps, and termites show far more cooperation and integration than the social aphids (Wilson 1971; Queller and Strassmann 1998). The haplodiploid ants, bees, and wasps have elevated within-colony relatedness because the haploid males deliver identical sperm to all their daughters. This means a colony with a once-mated queen will have average within-colony relatedness among the females of 0.75, and females are the cooperative part of the colony. However, the species that are most organismal often have lower relatedness among their members. Honeybee queens mate many times, which greatly reduces within-colony relatedness, but they are organismal (Seeley 1989). Each colony has a single queen who produces all the eggs. Activity is highly coordinated, from foraging to nest thermoregulation, and reproduction is through swarms. The greatest organismal conflict occurs when this colonial organism reproduces, when daughter queens kill for the right to be the sole queen, but this might be viewed as equivalent to parent–offspring or sibling conflict in standard organisms. The fungus-growing ant *Atta* also has organismal colonies headed by a single multiply mated queen (Boomsma and Ratnieks 1996).

Colony reproduction is not a group affair, as queens leave the mother colony to begin anew alone, carrying their starter culture of fungus, and defensive bacteria (Mueller et al. 2001). But *Atta* is more organismal than honeybees in at least one sense, that of having multiple worker morphologies (Hölldobler and Wilson 1990).

The term superorganism has often been used for some social insects (e.g., Seeley 1989; Wilson and Sober 1989; Hölldobler and Wilson 2008), but we do not see a compelling reason to use anything other than organism, as Wheeler originally did (Wheeler 1911). After all other organisms also originated as groups, some of them with genetically distinct members (e.g., eukaryotes), but we do not call them superorganisms.

The real challenge to viewing social insect colonies as organismal has come from their genetic diversity, and some resulting intraorganism conflict. Conflict can be over who lays eggs, when reproductives are produced, and the relative numbers of males and females. When conflict is strong enough, we would not consider the colonies to be organismal, and the line is of course difficult to draw precisely. But in some species, conflict is quite well controlled. In ant genera such as *Solenopsis* and the stingless bee *Frieseomelitta varia* conflict over reproducing is nonexistent, as their workers completely lack functional ovaries (Hölldobler and Wilson 1990; Boleli et al. 2000; Cruz-Landim 2000). In other species, such as the honeybee, physiological and behavioral suppression of some members by others, called policing, reduces actual conflict to a minimum (Ratnieks 1988; Ratnieks and Visscher 1989). When conflict is very low and cooperation very high, we think colonies should be viewed as organismal (Queller and Strassmann 2009).

EGALITARIAN ORGANISMS

Many organisms exist as single, fairly solitary cells, belonging to Archaea, Bacteria, and eukaryotic protists. The parts that constitute these organisms are their subcellular parts. Some alliances are so ancient that the contracts that went into forming them are no longer very accessible for study. Other parts may be more recently amalgamated.

The paradigmatic egalitarian organism is the partnership of the eukaryotic cell, comprised of at least the mitochondrion and the host cell, a collaboration that has resulted in an explosion of diverse and complex life forms. Despite the potential for occasional disputes over reproduction, with mitochondria and chloroplasts favoring producing daughters, no one would suggest that the eukaryotic cell is not organismal when it is independent, for example, a protist that is not embedded in a multicellular being. Eukaryotic cells clearly show that organisms can be formed from different species.

The prokaryotic cell provides a different kind of case. The very first cell might have come from the enclosure and joint reproduction of independent replicators, although it is also conceivable

that the elements could replicate properly only after they were combined, as in a hypercycle (Eigen and Schuster 1977; Maynard Smith and Szathmary 1995). Either way, subsequent history shows much combination from different species (Choi and Kim 2007). The case for egalitarian collaborations is strong because the genes in a bacterium are a mixture of ancient and recently arrived genes through horizontal transfer. Prokaryotes often innovate by taking adding foreign genes to their own.

We should not forget sexual cooperation; sexual partners taken together might also be organismal. The two partners bring genetic diversity to the progeny that result from their union. The more long term and exclusive the relationship, the more their interests converge toward organismality. Most extreme is probably the anglerfish species that have males that attach permanently to a female, fusing circulatory systems, and providing her with sperm to fertilize her eggs (Pietsch 2005). In this case cooperation is nearly complete and conflict is probably absent when only two partners are fused. Most other partnerships of mates fall far short of organismality, with conflicts over who should provide resources and the exclusivity of the consortship.

Conflicts may also occur between egg and sperm, but once a union occurs, it makes an organism. This seems like a fraternal union in the sense that two conspecific units fuse and bring the same genetic capabilities to the union. But the two individuals are usually unrelated, so both must reproduce, as in any egalitarian alliance. And, at least under anisogamy, they initially perform different roles, with the egg bringing most of the resources. But the most important point is that sexually created organisms firmly establish an interesting and overlooked precedent. Although the eukaryotic cell shows us that organisms can be formed from unrelated individuals (in this case different species), the sexual union shows that this need not be a rare historical event, that organisms can be reconstructed from unrelated individuals in every generation.

The last category of organism types is made up of two species. One might wonder how combinations of two species could ever be considered to be organismal. Such an organism should fulfill the same requirement of very low actual conflict and very high actual cooperation. Aphids are dependent on *Buchnera* for amino acids (Douglas 1998). *Buchnera* has one of the most reduced genomes and they rely on aphid genes supply what they have lost (Moran 2007). Is this dependence any different from dependence on specific genes within a genome for the same products? *Buchnera* is transmitted vertically through aphid eggs and conflict appears to be minimal.

Other two-species partnerships may not be as inextricably bound together as this case, but some can nonetheless be viewed as organismal. Lichens are made up of a fungal and an algal or cyanobacterial partner that is often acquired de novo from the environment (Honegger 1998; Piercey-Normore and DePriest 2001; Nelson and Gargas 2007). This partnership is so successful that

organisms in this group prevail overwhelmingly in the harshest, newest environments and lichens are at the root of many major fungal lineages (Lutzoni et al. 2001). The lack of coinheritance, genetic similarity, or great specialization on the part of the algal partner does not keep this partnership from achieving high cooperation with little cost. Other two-species partnerships that might qualify for organismality include fungus growing ants and their fungi, and perhaps other members of that partnership, and also squid and its light-producing *Vibrio* bacteria (Mueller et al. 2001; Nyholm and McFall-Ngai 2004).

The potential for conflict is higher here than in fraternal organisms, but the relevant question is the level of actual conflict, and this may be minimal in some cases. We know that genetic identity is not necessarily required by the existence of the eukaryotic cell, honeybee colonies, and indeed from every sexual union.

Some Groupings that Are Not Organisms

Although we are suggesting organismal status for some entities that are often not called organisms, it is important to note that our definition is not wildly permissive. Instead it is a strict one that also excludes some entities that have been claimed as organismal.

Many groupings that have some evident cooperation have far too much conflict to be considered organismal. At the extreme are claims for the biosphere or Gaia. Whatever homeostatic mechanisms may exist at this level, the reproductive conflicts among its constituents are profound, reflected in part by the prominence of competition in ecological texts. Coming down a level or two, the same problem clearly applies to claims that ecosystems or communities or species are organismal. Most mutualisms are less than organismal because they still have substantial conflict; we have simply suggested that we should be more open-minded about the possibilities for mutualistic organismality. Even among social groups of the same species, only the most extreme, like advanced social insects, should be considered organismal. Human societies in particular, although extreme in their types and levels of cooperation, have too much conflict to be considered organismal. This is not to say that cooperation and adaptation, where they exist at the level of any of these groupings, are uninteresting. But near unanimity of purpose needs to be present for them to be called organisms.

We also exclude some groupings because they lack sufficiently high cooperation. An aphid clone that is not a gall forming species is not normally organismal because the aphids do not do much for each other. They are genetically identical and have the same potential interests, but their actual behavior is not cooperative enough to be organismal. The same is true for other clones such as armadillo litters (Enders 2002).

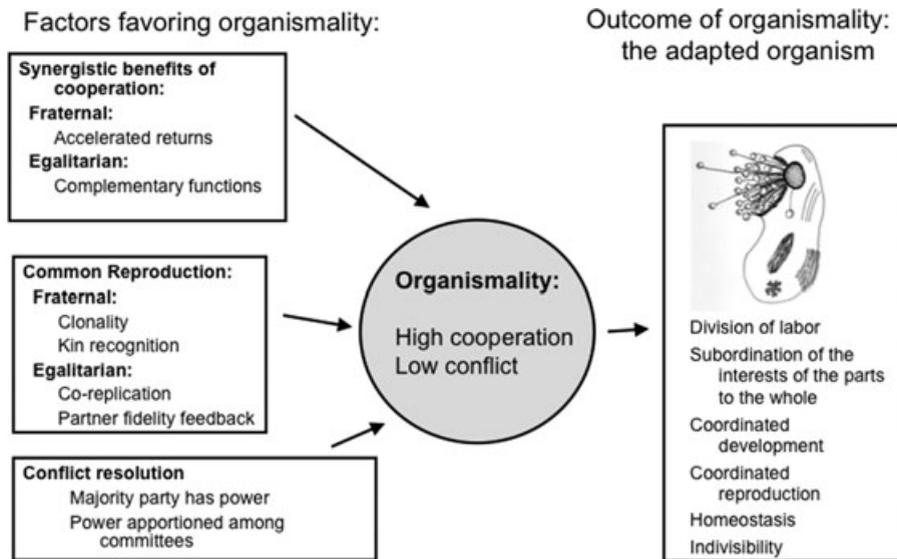


Figure 2. Diagram of factors favoring organismality and their consequences.

How Is Organismality Achieved?

What kinds of conditions result in organism-level binding of interests, with unanimity of interests and controlled conflict? In some ways this is the same question as the evolution of cooperation itself, but carried to an extreme. Here we sketch out three broad kinds of conditions that favor organismal bonds (Fig. 2). First, there must be synergistic advantages to cooperation that make it more than a zero sum game. Second, some conditions must largely align the reproductive interests of the parties. Finally, when potential conflicts remain, they must be suppressed by some mechanism for organismality to be achieved. These three factors favor organismality, but organisms are sufficiently diverse and complex that no one of them is an absolute blueprint for making an alliance into an organism (Fig. 2). In fact, fraternal and egalitarian organisms tend to follow different paths.

THE SYNERGISTIC BENEFITS OF COOPERATION

If cooperation is of the egalitarian form, with different kinds of partners, the initial synergistic advantage usually arises from an immediate division of labor. The advantages of acquiring a pre-built adaptation that would be unlikely to arise independently can be huge, as for example in the paradigm cases of the acquisition of mitochondria or chloroplasts. Squid can acquire luminescent bacteria that shine in the squid light organ. Aphids carry *Buchnera* in dedicated endocytes where the bacteria produce essential amino acids (Moran 2007). In each case, the smaller partners acquire a suitable, nutrient-rich home. Lichenized fungi acquire algae or cyanobacteria that exchange photosynthate for water balance and protection (Arnold et al. 2009). In fraternal associations, such immediate gains from division of labor are less likely because the units are of the same type. Therefore, at least the initial advan-

tage is more likely to come from advantages of scale, of having multiple units. In simple multicellular organisms, such advantages may come from predator avoidance; a larger clump of cells may be too much for a predator to handle (Boraas et al. 1998). In social insects, the greater returns to scale are also often the result of antipredator advantages, either through life insurance or fortress defense (Queller and Strassmann 1998; Strassmann and Queller 2007). Division of labor is of course also a strong feature of fraternal organisms, but it generally evolves after the association is formed, instead of being present from the beginning. In particular, fraternal organisms can evolve a reproductive division of labor that is impossible in egalitarian ones (the fraternal sub-components of such associations can have this, but the egalitarian partners cannot replace each other).

Even though some partners may give up reproduction in fraternal organisms, the requirement for net synergistic benefit remains. Among like units, reproductive sacrifice is favored under Hamilton's famous kin selection rule: $c < rb$ (the cost to the altruist is less than relatedness times the benefit to the beneficiary). Because r is no greater than one, the benefit must be greater than the cost (Hamilton 1964).

COMMON REPRODUCTION

The more tightly the interests of one partner can be bound to the interests of the other partner, the more cooperation is likely to prevail over exploitation, and the more organismal the system will tend to be. There are two primary ways that this can be achieved.

In fraternal organisms, relatedness is high, there is reduced potential conflict, and some individuals may reproduce on behalf of others. The most effective control may be the lack of genetic differences. When the component parts of an organism are genetically identical, the group's interest will be favored, and there

will be no lower level conflict to be controlled. This may be why it is nearly the rule that multicellular organisms are clonal, usually because they have gone through a single-cell bottleneck early in development, and why true chimerism is rare (Strassmann and Queller 2004). Even plants that develop from pieces of other plants, parts Harper calls ramets, go through meristems of rather few cells. It may also explain the lack of elaboration in major multicellular lineages that do have chimerism, such as the *Dicystostelia* (social amoebas or slime molds), which have similar and relatively simple body plans across an ancient lineage (Raper 1984; Schaap et al. 2006).

Social insect colonies have high relatedness among workers and brood, although often not so high as the maximum possible under haplodiploidy (Strassmann et al. 1989). High relatedness is promoted by a bottleneck at the initiation of the colony, often a single queen and her mate (represented as stored sperm). Species that are initiated by swarms have other relatedness elevating life histories (Queller et al. 1988). High relatedness reduces potential conflicts, but does not eliminate them entirely because social insect colonies are made up of genetically different individuals.

High relatedness is also furthered by preventing mixing or fusion with less related units. Simple barriers sometimes suffice. An *Oncothrips teperi* thrips colony inside its enclosed gall is an independent entity (Crespi 1992). Where barriers are imperfect, uniformity can be reinforced through self-recognition or kin-recognition mechanisms. Kin recognition of some form or another is overwhelmingly common in social insects, and in many other social organisms, including many that form societies and not organisms (Starks 2004). Conflict is most thoroughly avoided when the recognition mechanism tracks pedigree kinship through recognition cues that represent overall shared genes. This is because such a recognition system can favor cooperative behavior across the genome. Nursery species often learn the odor of their relatives during a sensitive period when they are young and in the nest and unlikely to encounter nonrelatives. This is true for wasps, ground squirrels, birds, and many other species (Fletcher and Michener 1987; Starks 2004).

Perhaps the most extreme form of kin recognition is that represented by the immune system. Tissue grafts are rejected if they do not come from genetically identical organisms in many animal species (Loeb 1937). The highly variable multiple histocompatibility (MHC) locus mediates this. Although this recognition is based on a single-gene family, the locus complex is so variable that it accurately tracks pedigree relatedness. If individuals are too similar, cancerous selfish cell lineages can be transmitted to others. This appears to be what is happening in the Tasmanian devil, which has a transmissible cancer that is putting the whole species into danger of extinction (McCallum and Jones 2006). In other species, like *Botryllus schlosseri*, matches need not be perfect for recognition and fusion, but imperfect matches result in

substantial conflict over contribution to gonadal versus somatic tissues (Grosberg and Quinn 1989; Pancer et al. 1995),

Egalitarian organisms do not have this relatively easy path to reduced conflicts because their parts are not related. But they can sometimes evolve mechanisms that yield common reproductive interests, specifically if the units are coreplicated in a coordinated, fair fashion. The organization of genes into chromosomes assures that all genes get copied at the same time, as does the synchronized division of chromosomes in eukaryotes. When all parties, in this case, genes, must get duplicated through the same pathway, their interests converge. The convergence does not have to be perfect for organismality to evolve, just as relatedness does not necessarily have to be one in fraternal systems. Mitochondria and chloroplasts are in different coreplicons (Crozier 1970; Cosmides and Tooby 1981) from nuclear genes because they are transmitted only through daughters and not through sons. But the shared path through daughters assures that the coreplicons can generally cooperate on survival and reproduction, even if they may have conflict over sex ratio.

At a higher level, many of the most organismal mutualisms have some degree of coreplication. *Buchnera* symbionts are passed on through aphid eggs. When young *Atta* queens fly out to found a new colony, they carry a bit of fungus from their natal colony. Fig wasps carry pollen from their natal fig to a new one. How often organisms can evolve in mutualisms that do not coreplicate is an open question.

REDUCTION OF CONFLICT: CONGRESSES, PARTIES, AND COMMITTEES

It is clear that reduction of potential conflict has been important in both fraternal and egalitarian organisms, by high relatedness and coreplication, respectively. But it is also clear that if organism members are not identical, there remains potential for conflict. This is true at all levels of organization. Therefore, additional mechanisms that reduce actual conflict are often important in the evolution of organismality.

Leigh (1971) used the metaphor of a parliament for the genes in an organism. This captures the sense that an organism is a cooperative entity because parliaments provide a means of reaching peaceful and cooperative decisions. It also recognizes that disputes can occur. Leigh used the parliament metaphor primarily to argue for the force of the majority. If a single gene did something that went against the interests of the other genes in the organism, it would be "outvoted" as the other genes were selected to suppress its effects.

While giving Leigh full credit for the metaphor, we would like to alter it slightly to reflect the current understanding of organisms as true social groupings in which separate members have come together. We will speak instead of "congress," whose root meaning suggests this coming together, where "parliament"

Table 2. Examples of congresses, parties, and committees with and without conflict.

Entity	Definition	Example 1	Example 2	Example 3
Congress	The organism: made up of cooperating units	Individual wasps in a colony	Cells in a <i>Dictyostelium</i> slug	Genes in an individual
Parties	Coreplicons: suborganismal groups that reproduce together	Workers, queens	Different clones	Nuclear genes, mitochondrial genes
Committees	Groups with power to affect various phenotypes	Egg laying (conflict); hygiene (no conflict)	Differentiation as spores (conflict); build spore coat (no conflict)	Sex ratio (conflict); hair color (no conflict)

derives from speaking. More important than this minor modification, we extend and modify the metaphor in three ways, by applying it to multiple levels and by adding two additional layers to the metaphor: parties and committees. A multicellular organism can be viewed not only as a congress of genes, but also as a congress of cells. An organismal honeybee colony can be viewed as a congress of individuals. And an organismal mutualism can be viewed as a congress of individuals from different species. At the lowermost level, however, all of them can still be viewed as a congress of genes (Table 2).

Within each of these congresses, we can usually identify “parties” or groups of members with the same interests or coreplicons (Cosmides and Tooby 1981). This is because in organisms, different sets of genes (or cells or individuals) are often reproduced through different, or partially different, pathways. The members of a party have the same genetic interests, but they will be partly different from the interests of members in other parties. Parties are what the previous section was largely about. Multicellular organisms are typically one-party groups of cells, but most other organisms have separate parties, and even multicellular organisms have them at the gene level. For example, maternally transmitted mitochondrial genes would do better under a female-biased sex ratio than nuclear genes. In a lichen, algal reproduction and fungal reproduction are often, though not always, achieved through different propagules. In haplodiploid social insects, queen genes are passed on equally through sons and daughters, whereas worker genes run more through the latter.

This last example brings up the point that party allegiances may sometimes shift on different issues. Although workers align against the queen on sex ratios, they may support her in the question of whether the queen or (other) workers should lay the male eggs. Nor are parties fixed over evolutionary time. For example, multiple mating by haplodiploid queens has the effect of largely erasing party differences over sex ratio and whether workers should be allowed to lay male eggs.

There can also be members of a congress with no real affiliation: they are parties of one who could also be called mavericks. Transposable elements seem to be like this. Although they are

similar in that they replicate through transposition, each element does so independently of the others, through different transposition events. None works on behalf of the others. Similarly, each laying worker, if not suppressed by other workers in favor of the queen, strive for their own gain rather than the collective gain of any party.

The party concept seems a necessary addition for Leigh’s majority to work, and also reveals some of its limitations. Consider an organism in which each gene (or cell or individual) had its own unique interests—all mavericks and no parties. Such a state of affairs might have occurred before genes were linked into chromosomes that divided together. And such a state of affairs applies to many current nonorganismal groups. If in one of these groups, one member does something deleterious to the rest, others will not easily evolve to suppress it, at least if there is any cost to the suppressing member. To do so would only lower the suppressor’s fitness relative to group members that do not suppress. Suppression is easy only when many members have their fates tied together in a party. For example, a nuclear gene that suppresses mitochondrial female-biased sex ratio loses no ground to the other nuclear genes, because they coreplicate. A worker is most likely to suppress the egg laying of other workers when she loses nothing to other workers, because she is already committed to the queen’s reproduction.

The party metaphor also makes it clear that numbers are not everything, that majority rule is not a foregone outcome. For example, in some mutualistic organisms, the parties may be fairly equally balanced; the alga and fungus in a lichen could have similar numbers of genes. Of course, one might argue that organismality is unlikely in this balanced scenario, that you need strong majorities to get agreement, but we prefer to leave that question open. A real example of balanced interests may occur when an organism’s maternal and paternal genes are imprinted and pursue different interests, for example, over the amount of resources to extract from the mother (Haig 1996).

Regardless of the balance between parties, outcomes depend on more than that. An organism is like a congress, with parties, where all the work is done in committees (parliamentary

ministries would reflect executive function even better, but are complicated by the fact that most members of a ministry are not members of the parliament). There are important committees, for example laying the down the basic body plan and less important ones, for example on hair color. Many involve no conflict between parties; some do. No analogy is perfect, however. Unlike most real congresses, membership on committees is not assigned. Instead, members join the committees where they are able to do the most good for themselves, doing something that gets them reelected (reproduced). As in real congresses, a member can be on multiple committees (pleiotropy) although serving on multiple committees could impair its effectiveness on any single committee (trade-offs).

What the extension of the metaphor to congresses speaks to, of course, is power. Different genes (or cells, or individuals) have different abilities to affect different traits. Power may flow from numerical advantages, as Leigh suggested, but also from other sources. In social insects, where conflict resolution has been thought about most, the numerical advantage of the workers may help them in some conflicts with the queen, for example over sex ratios (Beekman and Ratnieks 2003; Ratnieks et al. 2006). But just as important is the fact that workers populate the committees on brood care. On the other hand, although there is only one queen, she holds the only seat on the committee on the initial sex ratio and she can sometimes use that power to constrain the worker's choices.

Perhaps where the committee metaphor does the most useful work is with mutualisms. Numerical advantages may still sometimes apply; an aphid's genes presumably sit on a lot more committees than *Buchera* genes, and they may be able to control even those in which *Buchnera* is a member. But that does not necessarily mean that conflicts are necessarily unchecked in the many mutualisms in which the partners are more equally balanced.

Consider a legume and a *Rhizobium* partner. Committees on legume growth and differentiation are dominated by legume genes and committees on *Rhizobium* physiology are dominated by *Rhizobium* genes. Mixed membership occurs principally on a limited number of committees involved in the interaction of the two partners. The result could be considerable conflict in those areas, for example over how much nitrogen is provided to the plant or how much carbon to the bacteria. But another possibility is that each partner more or less fully controls certain aspects, that *Rhizobium*, which largely controls the committees on nitrogen production also has primary leverage over its disposition, and that the plant has similar leverage over carbon. In this scenario neither party may achieve its optimum, but a cooperative outcome without much conflict may still be reached. We do not assert that this is necessarily the case (for one thing we have neglected conflict among the bacteria)—only that we should be open to the possibility that potential conflicts might be well controlled even

without one partner completely dominating. The most exciting area in the evolution of mutualism is figuring out how the levers of power work and how they can lead, or not lead, to conflict reduction.

Conclusion

With respect to our definition of organismality, some questions remain. How should we quantify cooperation and conflict? Where does an organism begin and end in the life cycle? Can an organism belong to two species? With respect to the larger question of how such organismal entities evolve, even more questions remain. Some important features have been identified, but few seem to be universally important. Genetic relatedness is crucial in some organisms and not in others. But how many mutualisms are organismal and how important is coreproduction? How important is physical contiguity? Does membership have to be permanent? But despite these unresolved issues, the benefit of having removed them from the definition is that we become able to ask whether those factors have been in fact been important in the evolution of extreme cooperation.

The social view of the organism gives us a much broader view of cooperation. So much fruitful theory on social interactions has come from the study of animals, particularly, birds, mammals, and social insects. We have begun to apply and extend these theories to other animals, to fungi, plants, and, perhaps most importantly, to microbes of all kinds. But, on the face of it, cooperation seemed to be a modest part of the social universe. This changes once we understand that each organism is itself a social unit that has evolved very high cooperation. Cooperation is in fact extremely common. The organism is the frontier of the adapted world; inside it there is harmonious teamwork, outside it there is conflict and confusion.

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