Evolution: What Is an Organism?

Defining an organism has long been a tricky problem for biologists. Recent work has shown how an approach based on adaptation can solve this problem, giving a conceptually simple two-dimensional measure of 'organismality'.

Stuart A. West[1] and E. Toby Kiers[2]

T.S. Kuhn famously divided scientific progress into two stages [1]: first, there are the periods of scientific revolution or paradigm shift, when existing ideas are replaced with radically different ones; second, there are periods of 'normal' science, when all scientists work within an accepted paradigm, using it to solve puzzles. Contrary to Creationist efforts to publicise the contrary, evolutionary biology is in a period of normal science and puzzle solving. Even in normal periods, however, new ideas can be born that greatly alter your perspective on particular issues, challenging previous dogmas, or even making you appreciate a problem where you thought there was none: Queller and Strassmann's [2] recent reassessment of the organism is a good example.

Amongst biologists, there has been a lack of agreement on exactly what is required to make something an organism [3,4]. A common approach to defining an organism is to consider things that clearly are organisms, and to then determine the attributes making them what they are. This has led to a focus on characteristics such as indivisibility (if you cut an organism in half it cannot function) and genetic uniqueness (there is only one of each organism) [5]. The problem is that such approaches are heavily based on animal attributes; definitions become more slippery with smaller or more obscure taxa [2]. Furthermore, it is now appreciated that most of the major evolutionary transitions have relied upon previously independent groups of individuals coming together to form larger units, for example, replicators in chromosomes, cells in multi-cellular organisms, and workers within the eusocial insects [6,7]. Can and do 'organisms' occur at all of these evolutionary levels?

Queller and Strassmann [2] make adaptation, the seemingly 'goal-directed' process, the key aspect in the definition of an organism. The problem of adaptation is explaining why distinct parts of an organism appear contrived as if for the same purpose — namely how the growth, development and reproduction of that organism (and sometimes its kin) work in concert towards this shared goal [8]. Put another way, why is the living material that we call an organism packaged into units of common purpose [9]? The modern answer to this problem is: natural selection leads to organisms that appear designed for a single purpose, that purpose being maximization of their inclusive fitness [10,11].

Queller and Strassmann [2] turn this around, arguing that it is *exactly* this shared purpose that defines an organism. Specifically, something is an organism if the parts work together for the integrated whole, with high cooperation and low conflict. This means the organism is the largest unit of near-unanimous design. The 'near' is required because there can always be some conflict, even within the strongest examples of organisms, such as genetic conflicts within animals.

Given this argument, it then becomes possible to assess where any living thing stands on a scale of 'organismality', by considering two variables: the extent of cooperation, and the extent of conflict (Figure 1) [2]. Organisms are defined by when cooperation is high and conflict low. If both cooperation and conflict are high we have societies. If both conflict and cooperation are low we have simple groups. If cooperation is low and conflict is high we have competitors. Whilst it may be hard to accurately place specific cases on the scale, the elegance of this classification is that it is conceptually clear and simple. Where things fall on this two-dimensional continuum can be explored at several levels, and this is when things start to get fun (Figure 2).

Consider groups of cells (Figure 1A). In animals such as mammals, each individual cell develops from a single fertilised cell, leading to genetic uniformity, with minimal conflict and high cooperation. This is clearly an organism. However, mutation can bring conflict, such as cancerous growths. The potential for such mutations will be greater in larger, many-celled animals, leading to increased potential for conflict. A whale is therefore less of an organism than a mouse. In the Tasmanian devil, a fatal facial cancer is transmissible, increasing internal conflict, making them even less of an organism. Likewise, even some forms of cancer can be passed from mother to developing foetus [12]. In marmosets, cells mix between fraternal twins while in the uterus, also reducing organismicity [13]. So while they are at an extreme end of the organism continuum, not all animals are 'organismicly' equal.

Things get much more variable when considering other taxa such as plants, algae and bacteria. A particularly interesting example is provided by *Dictyostelium* slime moulds. These normally live unicellular lives in the soil, feeding on amobae; no one would think to call such a group of cells an organism. However, when times are tough, cells come together to form a fruiting body, with approximately a quarter of the cells sacrificing their lives to become the stalk cells that help spores disperse (Figure 2). How organismal is this fruiting body? The high cooperation and low conflict within the fruiting body, a result of high mean relatedness [14], suggests it should fall relatively high on the organismality scale. This means that groups of slime mould cells can be an organism, but perhaps only at certain stages of their life cycle! A remarkable range of cooperative behaviours are being identified in what are normally considered single celled organisms, such as bacteria and protozoa [15], providing other examples of possible organismality.

Now, consider groups of multi-cellular individuals (Figure 1B). In cases where the individuals all work together for a single purpose, they would be defined as organisms. A clear example is in the Portugese man o' war, a jelly-like marine invertebrate, where clones bud and can have specialised function within the colony. Similarly, within colonies of social insects, such as the honeybee or leaf cutter ants, there is low conflict and high cooperation, with individuals having specialised functions. These are sometimes referred to as superorganisms, but why not just call them organisms? From an adaptive perspective, a colony of social insects is analogous to the colony of cells that comprise a human.

Sexual partners are not usually thought of as an organism, with much reason. For example, bed bug males cause considerable harm to their mates when they violently pierce their body wall to inseminate them. Under this new classification, however, some sexual partnerships can be considered more organismal than others. In species such as albatrosses or dik-diks (a small African antelope), individuals mate for life, leading to low conflict and high cooperation, placing the pairs of animals appreciably up the organismality scale. An even more extreme example is provided by the species of anglerfish where the male fuses onto the female and basically becomes a ball sack. Queller and Strassmann [2] point out that while this relationship is often called parasitic, it makes much more sense to think of it as an organism, as the pair are essentially a single unit with a common goal.

Is there a danger that the term organism will be over-used? For instance, one could argue that all things clonal could now be classified as an organism. Dandelions are clonal, sharing both contiguity and genetic identify, but how do they rank on the organismality scale? Again, Queller and Strassmann's [2] classification system is quite pragmatic. They propose that dandelion clones are not highly organismal because members do not show high levels of cooperation. Consequently, members of a dandelion clone may be better viewed as direct competitors than organisms. Similarly, consider groups of animals such as shoals of fish: whilst there can be cooperation to avoid predators, there is still the potential for much conflict, and this prevents them scoring high on the organismality scale.

Finally, we can consider multi-species groups. It is now accepted that the mitochondria in eukaryotic cells originated via the incorporation of a bacterium. We have no trouble thinking of eukaryotic cells as an organism, or multicellular groups of such cells being an organism. Given this, it is only a small step further to consider other mutualistic associations, such as the *Buchnera* bacteria in the guts of aphids or the algae that provide carbon to lichens, as organismal, as they too are characterised by high cooperation and

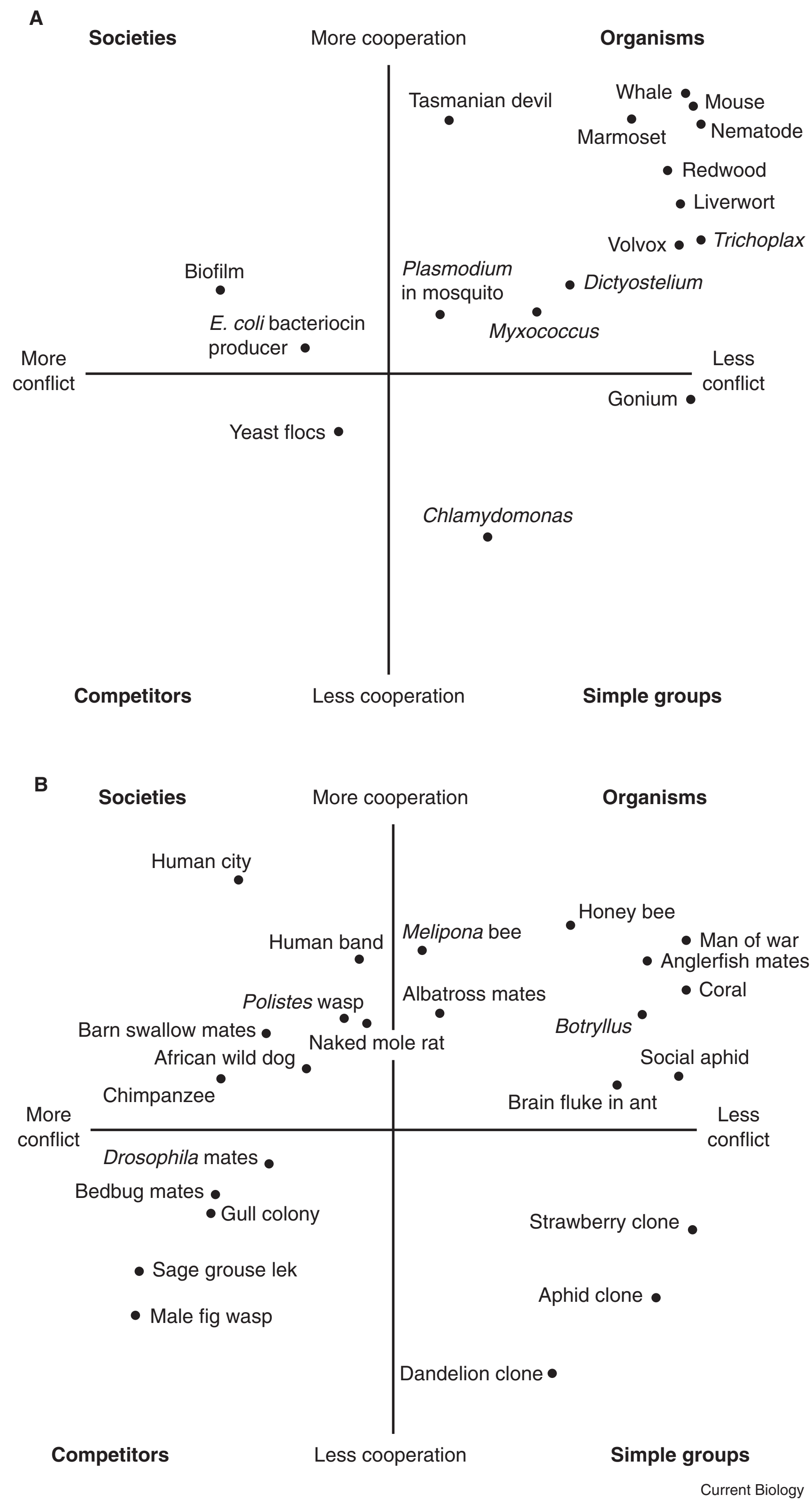

Figure 1. Queller and Strassmann's [2] two-dimensional measure of organismality.

Shown are examples for groups of cells (A) and groups of multi-cellular individuals (B). Higher cooperation and lower conflict leads to greater organismality [2]. (Figure provided by David Queller; reproduced with permission from [2].)

Figure 2. What is an organism?

The human is clearly an organism. The horse was an organism. But what about the bacteria now growing in the horse, the slime mould fruiting body on the horse's faeces, or the clumps of plants growing in the background? (Photos provided by Marshall Burke and Owen Gilbert.)

low conflict. In contrast, other mutualisms with more ongoing conflict, such as cleaner fish mutualisms [16] or pollination mutualisms, are ranked considerably lower on the organismality scale. Close physical proximity is not, however, a defining characteristic. In some situations, even in those mutualisms that are not physically cohesive, for example legume–rhizobia interactions, conflict is largely controlled [17], thereby increasing the organismality of the mutualism.

At this stage, it is useful to ask: why we should care? We can put things on a cooperation and conflict scale and say how organismal they are, but does this really matter? Many will not care, and it is unlikely to change what most biologists are doing on a day to day basis; however, the elegance of Queller and Strasmann's [2] classification is that it generalises from basic evolutionary principles to all levels of biological diversity. It is not biased to certain taxa, or to certain preconceptions. It basically says natural selection does this, and this will lead to things which we can call organisms.

Queller and Strassmann's [2] classification is not black and white, but neither are all organisms. Maynard Smith and Szathamry's [7] work on the major transitions emphasised the importance of rare events of great importance. Queller and Strassmann [2] build upon this, emphasising the gradual steps along the way. By focusing on an adaptive perspective, Queller and Strassmann's [2] approach is also closely linked with the theoretical formalisation of Darwin's theory of natural selection [18]. Recent theoretical work has addressed the related question of defining the conditions under which individuals can be selected to behave as if they are adapted to maximise the reproductive success of their group [9]. The answer is when there is no conflict within the group, which can occur due to high relatedness or repression of competition [9]. Queller and Strassmann's [2] approach emphasises that while reduced conflict can pave the way to organismality, it is only reached if there is also selection for high cooperation.

We would respond to the questions posed two paragraphs ago with the answer that yes we should care, and yes it does matters. The concept of the organism is fundamental to the study of adaptation [8]. By putting adaptation back into the concept of the organism, a firm evolutionary footing is provided to the organism concept, and a slew of interesting questions are raised [2,9]. Whilst it could be useful to have multiple definitions of the organism concept, the sooner that the adaptationist approach finds its way into text books, the better.

References

1. Kuhn, T.S. (1962). The Structure of Scientific Revolutions (Chicago: University of Chicago Press).
2. Queller, D.C., and Strassman, J.E. (2009). Beyond sociality: the evolution of organismality. Phil. Trans. R. Soc. Lond. B *364*, 3143–3155.
3. Wilson, J. (2000). Ontological butchery: organism concepts and biological generalizations. Phil. Sci. *67*, S301–S311.
4. Pepper, J., and Herron, M. (2008). Does biology need an organism concept? Biol. Rev. *83*, 621–627.
5. Santelices, B. (1999). How many kinds of individual are there? Trends Ecol. Evol. *14*, 152–155.
6. Leigh, E.G. (1991). Genes, bees and ecosystems: the evolution of a common interest among individuals. Trends Ecol. Evol. *6*, 257–262.
7. Maynard Smith, J., and Szathmary, E. (1995). The Major Transitions in Evolution (Oxford: W.H. Freeman).
8. Gardner, A. (2009). Adaptation as organism design. Biol. Lett. *5*, 861–864.
9. Gardner, A., and Grafen, A. (2009). Capturing the superorganism: a formal theory of group adaptation. J. Evol. Biol. *22*, 659–671.
10. Hamilton, W.D. (1964). The genetical evolution of social behaviour, I and II. J. Theor. Biol. *7*, 1–52.
11. Grafen, A. (2006). Optimisation of inclusive fitness. J. Theor. Biol. *238*, 541–563.
12. Isoda, T., Ford, A.M., Tomizawa, D., van Delft, F.W., Castro, D.G.D., Mitsuiki, N., Score, J., Taki, T., Morio, T., Takagi, M., *et al*. (2009). Immunologically silent cancer clone transmission from mother to offspring. Proc. Natl. Acad. Sci. USA *106*, 17882–17885.
13. Ross, C.N., French, J.A., and Orti, G. (2007). Germ-line chimerism and paternal care in marmosets (*Callithrix kuhlii*). Proc. Natl. Acad. Sci. USA *104*, 6278–6282.
14. Gilbert, O.M., Foster, K.R., Mehdiabadi, N.J., Strassman, J.E., and 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.
15. West, S.A., Diggle, S.P., Buckling, A., Gardner, A., and Griffin, A.S. (2007). The social lives of microbes. Annu. Rev. Ecol. Evol. Syst. *38*, 53–77.
16. Bshary, R., and Grutter, A.S. (2005). Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. Biol. Lett. *1*, 396–399.
17. Kiers, E.T., Rousseau, R.A., West, S.A., and Denison, R.F. (2003). Host sanctions and the legume-rhizobium mutualism. Nature *425*, 78–81.
18. Grafen, A. (2007). The formal Darwinism project: a mid-term report. J. Evol. Biol. *20*, 1243–1254.

[1]Department of Zoology, Oxford University, South Parks Road, Oxford OX1 3PS, UK.
[2]Institute of Ecological Science, Faculty of Earth and Life Sciences, Vrije Universiteit, De Boelelaan 1085, NL-1081 HV Amsterdam, Netherlands.
E-mail: stuart.west@zoo.ox.ac.uk

DOI: 10.1016/j.cub.2009.10.048