



puts researchers interested in theory and modelling in an ideal position.

If you knew earlier on what you know now, would you still pursue the same career path? I would have moved back into biology much earlier. I was seduced by money and career success in computers, so greed kept me staying there longer than I should have. I am more fulfilled thinking about and doing biology, although much poorer.

Who would be at your ideal conference? I'd love to be marooned on a desert island (with whiteboards, or at least a smooth sandy beach to scribble on) with Michael Lynch, Ralph Greenspan, Norbert Perrimon, John Mattick, Michael Wade, Thomas Whitham, Sara Via and Allen Moore. Perrimon, Mattick and Greenspan each have their own unique perspectives on how complex gene networks might work, while Whitham, Wade and Moore extend evolutionary network thinking to social and ecological communities. Via and Lynch are the brilliant sceptics whose smart null hypotheses keep everyone else grounded in facts. I'd like to hear this group discuss how natural selection affects the interaction of molecular/genetic and ecological networks.

Do you have a scientific 'hero'? If I had to choose just one, it would be E.O. Wilson. I highly recommend his autobiography to early career scientists.

What is the importance of theoretical and computational approaches in biology? I'm biased:

the most important work in biology today is being done by reductionist cell and developmental biologists who find out how life works, one hard-won fact at a time. However, their discoveries sometimes seem to make an enormous scree pile of loosely connected nuggets of information. The job of theoretical biologists is twofold: first, to discern pattern in the mountain of facts and propose testable hypotheses which simplify the mountain's structure; and second, to apply quantitative methods from theory to sharpen the analysis of experimental data. The second job perhaps carries less prestige in the theoretical community but arguably is as important as the first. Computational biologists add one more task to the list: building the data and information rich systems which facilitate access to and use of the mountain of facts.

What do you think about the 'electronic revolution' in publishing? The value of online tools will only increase with time as the mountain of facts grows higher and broader. This is why it is essential that information be freely available: the public pays for most non-proprietary research, and should have full access to it (after the shortest blackout period compatible with keeping for-profit journals in business). Freedom of access alone is not enough, however: structured repositories for data sets large and small are essential and use of them should become mandatory.

What ethical obligations do biologists have? Our first ethical obligation is education of the public and decision makers. The gap between what science understands and what the public comprehends grows ever larger. Lawmakers don't understand the scientific method, with its inherent uncertainties and lack of dogmatic answers to complex questions. They need our help. Talking about the role of researchers in public policy Daniel Pauly recently remarked that providing impartial, relevant, expert advice both to governments and to the interest groups which pressure them is where biologists can have the greatest impact.

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Quick guide

Bacterial predators

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What are bacterial predators?

Alfred Tennyson's oft-quoted phrase "nature red in tooth and claw" starkly reminds us of the prevalence with which some animals hunt, grab, tear, kill, dismember and eat other animals. Unbeknownst to the great poet, his word craft also figuratively alludes to predatory violence amongst unseen microbes. (Although "nature slimy in adhesin and lysin" more literally describes predation by bacteria, it doesn't quite pass poetic muster.) Despite some debate about the semantics of bacterial predation, here we shall consider as predators any bacteria that kill other microbes and consume them as a nutritional resource.

How common is bacterial predation? Dozens of predatory bacterial species, representing a wide range of taxa, have been identified, but much remains to be learned about the full diversity of predatory bacteria and the mechanisms by which they encounter, kill and consume their prey. Bacterial predation occurs in terrestrial, marine and extreme environments.

What features do bacterial predators share? All predatory bacteria have the ability to degrade the polymeric compounds that compose their prey, and most species engage in some form of active motility, which allows them to 'search' for prey rather than merely wait for accidental encounters.

How do distinct modes of bacterial predation differ?

Predation by bacteria can be either a facultative or an obligate mode of resource acquisition. Predator attacks can be made by individuals or by social groups — bacterial 'wolfpacks'. Mechanistically, bacterial predators can attack their prey either by some form of cell-cell contact, or remotely by the action

of diffusible secreted compounds. Obligate bacterial predators, such as *Bdellovibrio bacteriovorus*, engage in contact-mediated predation and tend to be small in size relative to their prey.

How does individual predation via cell-cell attachment work?

Individual predators that kill their prey only after directly attaching to the membrane of the prey cell can be epibiotic or endobiotic. Epibiotic predators secrete enzymes directly into the interior of their victim and then assimilate hydrolysed molecules from the interior of the prey cell. Examples include a *Vampirovibrio* species that feeds on eukaryotic *Chlorella* cells and *Vampirococcus*, which sucks the cytoplasm out of *Chromatium* bacteria. Endobiotic predators, such as *B. bacteriovorus*, enter prey cells to feed and divide inside of them. These bacteria attach to the cell wall of prey they collide with, penetrate to the interior and from there hydrolyse prey-component polymers and assimilate the by-products. Endobiotic predators can be distinguished with respect to whether they divide within the cytoplasm or periplasm of the prey (for example, *Daptobacter* and *Bdellovibrio* spp., respectively).

How does bacterial wolfpack predation work?

Social bacterial predators, such as *Lysobacter* spp. and members of the myxobacteria like *Myxococcus xanthus*, tend to attack prey as groups, even if they are capable of doing so as isolated individuals (as *M. xanthus* is). Such group predation can be accomplished remotely via the secretion of diffusible compounds that kill and decompose hapless neighboring prey. Alternatively, some predatory compounds may be attached to the predator cell surface or embedded in the extracellular polysaccharide matrix of the predator pack, and only function to despatch prey cells when they are close to the predator cells. Although wolfpack predation is normally envisaged as a predator swarm that invades and decimates a prey colony on a solid surface, some pack predators (for example, *Myxococcus* spp.) can surround and entrap their prey as a group even in

aquatic environments. Microbial group predation may be positively density dependent under some conditions.

The production of diffusible predatory compounds has profound social implications. The breakdown of prey cells by such secreted weapons creates a 'public good' in the form of consumable nutrients from dead prey. Any nearby cell resistant to predatory lysis can potentially utilize this public good, even individuals that did not contribute to the kill. Because enzyme secretion is costly, such remote predation is likely to be a trait that can be exploited by genotypes — 'cheats' — that do not themselves produce predatory enzymes.

How did bacterial predation evolve?

Facultative bacterial predators are thought to have evolved from saprophytic ancestors that earned a living by hydrolyzing polymers from already dead organisms. Saprophytes would only have needed to add the ability to kill living cells to their proficiency at decomposing organic polymers. Obligate predators presumably evolved from facultative intermediates. Although most characterized predatory bacteria belong to the Gram-negative Proteobacteria — and are represented in α , β , γ and δ subdivisions — they can also be found among the Chloroflexi, the Cytophagaceae and Gram-positive bacteria. Thus, bacterial predation appears to have evolved numerous times independently.

It has been proposed that endosymbiotic associations, the endosymbiotic precursor to mitochondria in particular, might have originated from the ability of some bacterial predators to attach to and enter prey cells. Such a model requires an explanation of how an initially predatory relationship evolved into a mutualism.

Are bacterial predators specialists?

Only in some cases, as prey range breadth can vary dramatically. For example, *Aristabacter necator* and *M. xanthus* can both feed on a wide variety of bacterial species and some fungi as well. In contrast, *Micavibrio admirantus*, an α -proteobacterium

and epibiotic predator, was reported in one study to have fed on only one bacterial species (*Pseudomonas malthophilia*) out of more than 50 tested. Other bacterial predators such as *Cytophaga* spp. have limited prey ranges as well.

Why should we study predatory bacteria?

There have been few rigorous studies of the ecological roles of predatory bacteria, but their common occurrence in diverse habitats indicates that, like bacterial viruses, they are important determinants of microbial community structure, diversity and dynamics. One study documented increases in bacterial predators of cyanobacteria during large declines of cyanobacterial blooms in a Canadian lake. Another showed that one species can be either predator or prey, depending on who it interacts with. More intensive study of bacterial predation will be critical for understanding microbial trophic webs.

A variety of plant and animal pathogens are susceptible to bacterial predators and study of these relationships may lead to unexpected medical, veterinary and/or agricultural applications. For example, experimental selection for enhanced killing efficiency by predators consuming pathogen populations may generate novel antibiotic compounds and biocontrol agents.

Finally, because of their rapid growth, ease of handling and small size, predatory bacteria offer tremendous opportunities for testing hypotheses about the ecology and evolution of predator-prey relationships and the roles of predators in determining community structure. Just like bacterial viruses, predatory bacteria show great promise for becoming model systems for controlled ecological and evolutionary experimentation.

Where can I learn more?

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