Threatened: Most species of albatross are declining dramatically as a result of long-line fishing techniques which a new campaign believes can be easily changed. (Picture: Oxford Scientific Films.)

how to reduce the number of albatross deaths caused by long-line fishing.

One task force member on board a tuna long-line vessel operating out of Cape Town witnessed 12 albatrosses being caught in a two-week fishing trip. Practical demonstrations at sea encourage fisherman to use relatively simple things such as streamers tied above the lines, which drastically reduce the number of birds killed.

Land-based workshops also help fisheries managers to understand the impact on albatrosses and other seabirds. The task force has been training onboard observers, who can monitor the number of birds killed and report on how effective any measures taken to reduce the number of deaths are.

There are 21 species of albatross with 19 under threat of global extinction: 2 are critically endangered with the Amsterdam albatross reduced to just 17 pairs; 7 species are endangered; and 10 more are listed as vulnerable.

The birds' normal lifespan is 30–60 years and most species are monogamous, taking around 10 years to reach breeding age and raising only a single chick every one or two years.

The RSPB is also pressing the UK for greater effort to conserve wildlife on its 14 overseas territories, a legacy of the country's empire, which are major wildlife centres. Many of these territories are in the southern hemisphere and include the breeding sites of one third of albatrosses. "At least £10 million is needed every year to protect and restore the rich biodiversity of these remote islands," says Graham Wynne, chief executive of the RSPB.

People in these territories are dependent utterly on biodiversity, Wynne says. "Tourism and fisheries are their main sources of income." Gough Island, part of Tristan da Cunha, is arguably the most important seabird island in the world, supporting millions of pairs of more than 20 species, including the endangered Tristan albatross, says Wynne. The impact of introduced invasive species such as mice and rats are further threatening these species in their breeding grounds. Their impact has been "devastating", he says.

When the RSPB asked British schoolchildren about albatrosses, they were shocked to find that none of them knew what one was. Their imagined drawings of these threatened birds feature in the new advertising campaign.

Spite

**Andy Gardner[1] and
Stuart A. West[2]**

What is spite? Spite is one of the four basic social behaviours. Social behaviours are classified according to the fitness consequences for the actor and its social partners (Figure 1). The four social behaviours are: mutual benefit, where both the actor and recipient benefit; selfishness, where the actor benefits at a cost to the recipient; altruism, where the recipient benefits at a cost to the actor; and spite, where both actor and recipient suffer a loss.

How can spite evolve? It is easy to see why mutual benefit and selfishness evolve, as this directly benefits the actor. Altruism and spite are trickier, because the actor's fitness is reduced by its behaviour. These puzzling behaviours can be explained by kin selection. This is where social partners share genes in common, so the impact of social behavior on the fitness of a social partner may be important. Famously, Hamilton's rule states that altruism will be favoured when the cost to the actor ($c > 0$) is smaller than the benefit (b) to the recipient multiplied by the relatedness of the recipient to the actor (r), that is, when $rb > c$. Altruism has been a major focus of attention among evolutionary researchers over the last four decades. It is less well known that Hamilton's rule can be twisted to show that spiteful behaviour is favoured when the cost to the actor ($c > 0$) is smaller than the product of the negative benefit ($b < 0$) to the recipient and negative relatedness ($r < 0$) of the recipient to the actor, so again, when $rb > c$.

How can social partners be negatively related? Genetic relatedness is a statistical regression measure that describes genetic similarity between two individuals, relative

to a reference population. In short, positive relatedness implies that two individuals share more genes than average, and negative relatedness implies that two individuals share fewer genes than average. Negative relations may often come into social contact with each other. The problem is: how can an individual identify its negative relations, and ensure that any spiteful behaviour is directed mainly at them? One solution is kin discrimination, where the actor recognizes its genealogical kin who are statistically more related than average (positive relatedness), and hence those individuals not identified as kin are less related than average (negative relatedness). The more kin that the actor can identify, the more negatively related it will be to everyone else. If relatedness to the victims of spite is sufficiently negative, then spite can be favoured by kin selection. This negative relatedness is expected to be very small in large populations, unless the actor can identify a huge number of kin. However, if individuals mainly compete locally with social partners then relatedness measured relative to the average competitor can be strongly negative even in very large populations.

An alternative mechanism, conceptually similar to the kin discrimination approach, is when individuals can estimate genetic relatedness directly, in the absence of kinship cues. If a gene coding for a distinctive trait (such as a green beard) is genetically associated with the spite gene, then the actor can pick out its positive and negative relations using this distinctive marker as a guide. By limiting spiteful behaviour to individuals that do not share the same marker, the actor ensures that its victims are sufficiently negatively related. However, so-called 'greenbeards' are predicted to be rare, because selection will favour other genes in the genome that disrupt this mechanism. Also, positive-frequency dependent selection acting on spiteful greenbeards either drives them

		Effect on recipient	
		+	−
Effect on actor	+	Mutual benefit	Selfishness
	−	Altruism	Spite

Current Biology

Figure 1. A classification of social behaviours.

to extinction or to fixation, and if everyone in the population has a green beard then there is no one to be spiteful to. Hence, greenbeard spite is expected to make only transient appearances during evolutionary time.

Where should we expect spite? Spite is predicted whenever individuals are able to identify negative relations. Negative relatedness will be strongest if individuals are good at recognizing positive relations, either through kin discrimination or greenbeard mechanisms, and also if there is local competition between social partners. We should therefore look for spite wherever individuals interact with kin and non-kin in highly competitive environments. However, even very weak negative relatedness can allow for spite when the cost is small or absent. It has been suggested that the social insects might provide nice examples of spite, particularly among the sterile castes. A non-reproductive worker has nothing to lose in terms of future reproductive success when it commits to a spiteful act.

Are there any examples of spite? The social lives of bacteria present some amazing examples of spite. Some bacteria explode in a shower of antibacterial toxins (bacteriocins) in order to kill their competitors (Figure 2A). Genetic linkage between the toxin gene and a gene conferring immunity to the toxin means that the closest relatives of the suicidal cell are spared, and only those cells that are negatively related are killed. This bacteriocin warfare has been observed in every bacterial species in which it has been looked for. This has interesting implications for health,

because if pathogenic bacteria are busy warring with each other then they are less able to sustain a vigorous infection. Spiteful bacteria can also be bad news for their hosts.

The phenomenon of cytoplasmic incompatibility, whereby male insects carrying the bacterial parasite *Wolbachia* sterilize mating partners who do not carry the bacterium, has also been described as a spiteful trait (Figure 2B). It has long been appreciated that inbreeding avoidance generates negative relatedness between mating partners, and although this may usually be very weak, it is strong enough to select for spiteful behaviour in this system because males do not transmit *Wolbachia* and hence this behaviour carries no cost to the spiteful bacterium.

Animals, too, can be spiteful. A nice example of greenbeard spite has been found in the red fire ant, where workers who carry the spiteful gene kill prospective queens who do not share the gene (Figure 2C). In this way, the workers ensure that the surviving queens are carriers of the gene. Interestingly, individuals that carry two copies of the spite gene are inviable. This results in balancing selection and hence the gene cannot sweep to fixation, which is why we are still able to observe acts of regicide directed towards queens who do not carry the gene.

Recently, it has been suggested that the soldier caste of the polyembryonic parasitoid wasp *Copidosoma floridanum* is an example of spite that is favoured due to localised competition (Figure 2D). These wasps develop within the bodies of moth caterpillars, and burst out when they have become adults. Some embryos develop precociously into snake-like soldiers, with
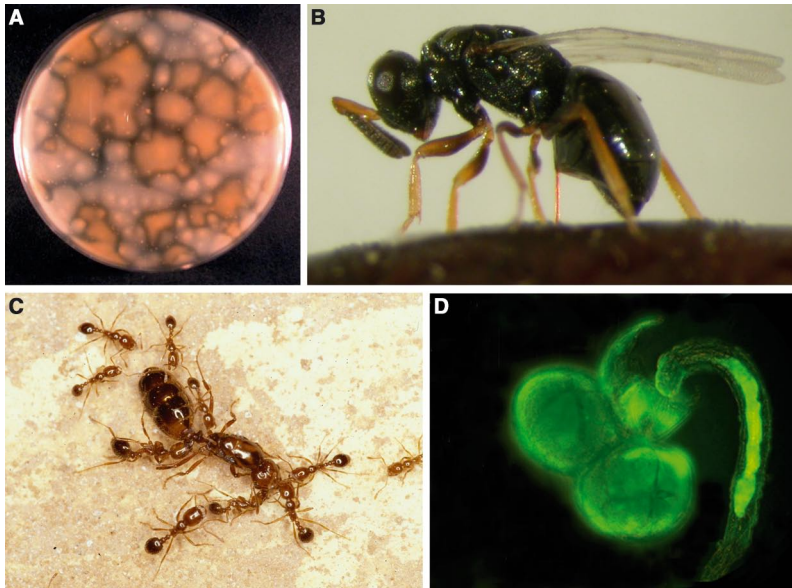
Figure 2. Examples of spite. (A) Two strains of the bacterium *Photorhabdus lumine-scens* (pink versus orange) engage in chemical warfare. Note the inhibition zones (bacterial no-man's land) that appear when colonies of the opposing strains meet. (Photo by R. Massey.) (B) The bacterium *Wolbachia* causes males to spitefully sterilize females in many species of insects, including the parasitoid wasp *Nasonia vitripennis*, pictured. (Photo by D. Shuker and S. West). (C) Red fire ant workers execute a queen who carries the wrong genes. (Photo by J. All and K. Ross). (D) A suicidal soldier of the parasitoid wasp *Copodisoma floridanum* murders and eats her embryonic hostmate (Photo by J. Johnson, D. Giron, and M. Strand.)

large mandibles, that pass their time in the caterpillar by killing regular embryos — including their siblings — before dying themselves. Usually, it is the females who are most spiteful, and their attacks are concentrated mainly on brothers and unrelated males. Hence, there are important implications for sex ratio evolution in this system.

Are there other ways of explaining these behaviours?
Spiteful behaviours have sometimes also been interpreted as a form of altruism or indirect altruism. Mutually harmful behaviours are favoured if they result in a benefit for some third party that is sufficiently related to the actor. Here, there is no requirement for negative relatedness to one's victims, and so a distinction has been made between so-called Hamiltonian spite that does rely on negative relatedness and Wilsonian spite that does not. However, this distinction may be more semantic than real, as one can often switch between these two views when considering a particular example of spite, depending on how one chooses to measure genetic relatedness between the perpetrators and the victims of spiteful behaviours.

Where can I find out more?
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Sex ratios and social evolution

David C. Queller

When we think of modern biology, an image that does not usually come to mind is of an entomologist squinting over mounds of wasps, sorting out the males from the females, and assiduously tallying them up. This work requires no fancy machines, no chemicals, no molecular techniques. But what it does rest on is a theory, and such seemingly pedestrian work has tested and confirmed one of the most elegant and successful theories in modern biology.

The ratio of females to males in a species is a topic that interested Darwin, but how such ratios evolve left him puzzled. The basic solution to the problem has led to a body of work that has informed nearly every important area of social evolution: group selection, kin selection, parent–offspring conflict, evolutionary stable strategies and game theory, and within-genome conflict.

The Düsing–Fisher model
The solution of the sex ratio problem has traditionally been attributed to Sir Ronald A. Fisher's 1930 classic *The Genetical Theory of Natural Selection*. But it is now known that a German biologist, Carl Düsing, got the solution more than four decades earlier. Fisher's book was the pipeline through which the theory flowed into the modern era, but his research reputation will now have to rest on other accomplishments, such as inventing the analysis of variance and deriving the fundamental theorem of natural selection.

The sex ratio argument, modernized and simplified a bit, goes like this. Natural selection is about reproduction. A gene affecting sex ratio does not affect your number of offspring;