Evolution

Genetic Invasion of the Insect Body Snatchers

By controlling sex and survival, some parasites can turn their hosts into new species

by Jack Werren

My first encounter with a jewel wasp in the wild occurred along a roadside in the mountains of Utah. I had stopped to investigate a porcupine that had been run over several weeks previously. Flies had long since arrived and done their handiwork. All that remained of the original animal was skin, bones, and quills. Beneath the skin, thousands of fly larvae had pupated and were metamorphosing into adults. But another organism was doing to the flies what they had done to the porcupine. This was the jewel wasp, *Nasonia vitripennis*.

Small (about 3 mm long) and gnatlike, the jewel wasp is unremarkable to the naked eye, but seen through a microscope, it is a beauty. Its finely faceted body shimmers with iridescent colors that change with the angle of light. A female jewel wasp seeks out fly pupae and kills them by injecting them with venom. She then lays twenty to forty eggs in each fly puparium. The eggs hatch into larvae one to two days later and begin to devour the meal provided by their mother. In about two more weeks, the adult wasps emerge. The short-winged, flightless males mate and die in the patch of fly pupae they were born in. The newly emerged winged females fly off immediately after mating in search of fresh fly pupae in which to lay their eggs.

What originally attracted me to these creatures was the female's ability to control the sex of her offspring. In wasps, bees, and ants, males develop from unfertilized eggs and are haploid (that is, they have just one set of chromosomes, inherited from the mother), whereas females develop from fertilized eggs and are diploid (with two sets of chromosomes, one from each parent). After mating, the female jewel wasp stores sperm in a special organ called a spermatheca. This organ resembles a balloon with a strawlike tube at one end; attached to the tube is a muscle that can either straighten out and allow sperm to pass to the egg (resulting in a daughter) or can crimp the tube and block the sperm (resulting in a son). How many daughters a female produces depends on a number of factors, including whether she is the first wasp to lay eggs in a fly pupa (in which case she'll lay mostly daughters) or the second (in which case she will lay more sons).

Despite the female's impressive ability to influence the sexual identity of her progeny, her control is far from complete. The jewel wasps, like the porcupine and the fly larvae before them, are themselves victims of parasites. They harbor an assemblage of genetic parasites that can alter an insect's reproductive system for their own advantage.

The jewel wasp is not alone in this. As scientists have discovered over the last decade, virtually all organisms carry genetic parasites that perpetuate themselves at the expense of their host. Some of these parasites are bacteria "inherited" from one generation to the next through the host or-

These minute jewel wasps, seen here against grains of sand, are parasites that are themselves victims of parasitic bacteria and parasitic DNA.
Ed Bridges

ganism's eggs (*see* "Feminist Bacteria of Ladybird Beetles," page 32). Others are actual pieces of DNA that reside in the host organism's chromosomes. For example, in most organisms small, mobile pieces of DNA called transposons make and insert extra copies of themselves in the chromosomes of their hosts. Humans have hundreds of thousands of copies of a transposonlike element called Alu that makes up more than 5 percent of our DNA. This parasite is relatively benign, although every once in a while it causes a harmful mutation by inserting itself in the wrong place. Other organisms, such as mosquitoes, mice, and fruit flies, have parasitic chromosomes that are able to insure that they end up in all the host's reproductive cells, rather than just half, as would normally occur during meiosis.

What makes the jewel wasp unusual is the variety of genetic parasites it harbors and the severity of their effects. Not all individuals are infected with all these parasites at any given time, but among those commonly found are bacteria that kill male embyros; a second element (which we have not identified yet) that is transmitted only through eggs and that causes the wasp to produce nearly 100 percent daughters; and a bacterium called *Wolbachia* that prevents the development of hybrid offspring engendered by the mating of jewel wasps with wasps of closely related species. But the most remarkable piece of parasitic DNA found in the jewel wasp is the paternal sex ratio chromosome, PSR for short.

PSR is a killer chromosome. Diminutive—about one-fifth the size of a regular chromosome—it is found only in some males of the species. PSR hitches a ride in the spermatozoon along with the other chromosomes. Just as picking up human hitchhikers can sometimes be dangerous, sharing a sperm with PSR is fatal for its fellow travelers.

After an egg is fertilized, PSR destroys all the other paternal chromosomes, causing them to condense into a mass, which is eventually lost during development. PSR alone survives to join the maternal chromosomes within the egg. Without the fratricidal action of PSR, the egg would have been diploid, and the fertile embryo would have developed into a female. With PSR on board, the fertilized egg will remain haploid and produce a male. This sex change is advantageous for the parasite because PSR in male wasps is transmitted to 100 percent of the spermatozoa (and thus to the next generation). But PSR stuck in a female tends to get lost during meiosis and reaches significantly less than 50 percent of her eggs.

PSR is not only a killer of chromosomes; it is also a serial killer. In each generation, it becomes associated with and destroys a new set of chromosomes, converting females into males. Because this chromosome is so deadly, inevitably eliminating all the chromosomes with which it is associated, generation after generation, it is considered the most extreme example of parasitic DNA so far identified from any species.

Genetic parasites such as PSR challenge our basic concept of what an organism is. For example, PSR is part of the jewel wasp's DNA, but it is harmful to the rest of the genetic material. We now know that most organisms contain a variety of parasitic DNAs. Certainly an organism's genome is not a completely cooperative unit, as we used to think. There is conflict within the genome.

How does such genetic conflict begin? For instance, where did PSR come from? Trying to answer such questions brought me back, somewhat circuitously, to *Wolbachia*. All the jewel wasps I have collected from the wild carry these intracellular bacteria, which reside in cells of the male and female reproductive tract. The bacteria can be quite numerous: jewel wasps typically harbor one to two thousand in every egg.

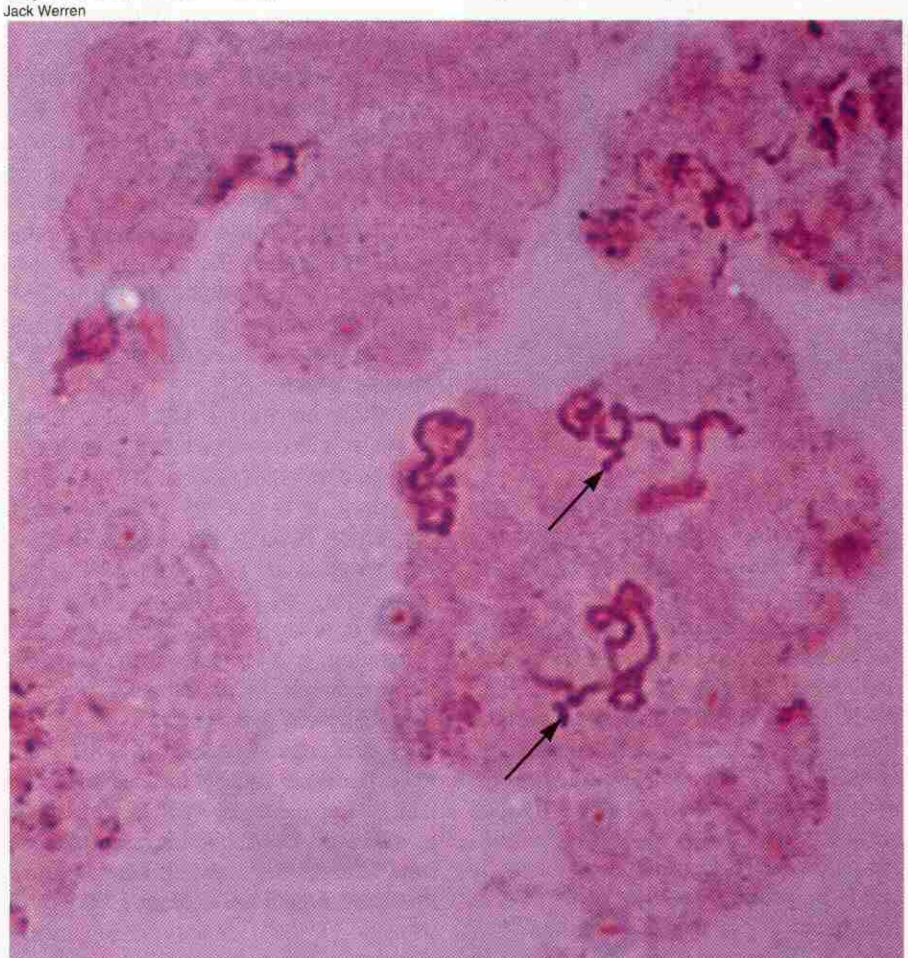
At first glance, *Wolbachia* would appear to be simply going along for the ride. However, when we cure insects of the bacteria by treating them with antibiotics or arrange matings between insects carrying different strains of *Wolbachia*, we find that the bacteria exercise considerable control over the insects' reproduction. *Wolbachia* bacteria in a male's testes cannot be transmitted via the sperm, but they do modify his chromosomes, probably by producing proteins that bind to the sperm's DNA. Unless bacteria of the same strain are also present in the egg to undo this modification, the sperm-delivered chromosomes will fragment and be destroyed in the fertilized egg. For most insects, this results in the death of the embryo. In the jewel wasp, the outcome is less than lethal: it results in (haploid) males.

The bacteria benefit indirectly because eliminating the daughters of females who do not have the same bacterial strain actually increases the frequency of that strain in the population. By this mechanism, infected females can eventually predominate, as is seen in populations of jewel wasps and many other insects.

Some scientists have speculated that control by *Wolbachia* over the insects' reproduction may be important in the evolution of new species. A key step in speciation is reproductive isolation of populations, which allows them to evolve in divergent directions. If bacteria cause reproductive incompatibility between populations that once interbred, bacteria may also promote speciation.

In these developing jewel wasp sperm cells, the stubby, darkly stained PSR chromosomes (see arrows) lie next to the larger, lighter chromosomes that they will ultimately destroy.

Jack Werren



The situation in jewel wasps suggests this may indeed happen. *Nasonia vitripennis,* which lives throughout the world, has two close relatives in North America: *N. longicornis,* in the west, and *N. giraulti,* in the east. The cosmopolitan *N. vitripennis* overlaps with the two others in some places, making hybridization between them a real possibility. In our lab, we have found that while the three different species of jewel wasp will mate with one another, no hybrid progeny result. Closer examination reveals that chromosomes from sperm are chopped up into little pieces in the fertilized egg. However, when we cured the wasps of their *Wolbachia* infections and repeated the crosses, true hybrid progeny developed. In other words, reproductive isolation is "curable."

What does all this have to do with PSR? Occasionally in incompatible crosses a piece of chromosome survives the fragmentation process and is passed on to the next generation. Bryant McAllister, a graduate student in my laboratory, has found that DNA sequences on PSR are much more similar to DNA from *N. longicornis* than to DNA of the jewel wasp, indicating that PSR is an "alien chromosome" that came from the former species during an incompatible cross. One of the pieces of PSR DNA that McAllister has studied is itself a transposon, which makes it a piece of parasitic DNA on a piece of parasitic DNA, generated by a parasitic bacterium within a parasitic wasp. PSR may owe yet another debt to the *Wolbachia*—its ability to destroy chromosomes. We are now testing the possibility that PSR acquired the relevant genetic material from *Wolbachia* by genetic exchange during formation of the chromosome.

Wolbachia are turning out to be quite common in insects. During one trip to the rain forests of Panama, for example, I collected and examined more than a hundred species and found that more than 5 percent were infected with *Wolbachia*. Extrapolating to the global insect fauna, which is currently estimated to be at least five million species, an amazing 250,000 species may be infected with *Wolbachia*. Only time will tell whether these reproductive parasites are important in the evolution of new species, but the possibility is tantalizing. At any rate, I have had to give up my conception of an organism as a strictly cooperative unit. When I peer through a microscope these days, I am no longer even certain where one organism ends and another begins.