EDITORIAL

Nasonia: a jewel among wasps

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This issue contains a collection of papers on the parasitoid wasp *Nasonia vitripennis*, many of which were prompted by the publication of its genome sequence as well as that of two closely related congeners (The *Nasonia* Genome Consortia Werren *et al.*, 2010). This issue focuses on the evolutionary aspects of *Nasonia* research, whereas a special volume of *Insect Molecular Biology* presents recent work on the molecular findings of the *Nasonia* Genome Project. This short essay explores why people are interested in this tiny insect—the back story—and then briefly asks how the genome sequence will affect future research using the wasp.

First, some taxonomic and natural history context. The Hymenoptera—the ants, bees and wasps—are one of the four great mega-diverse orders of insects, the other three being beetles, moths and flies. The Hymenoptera are divided into three main divisions, and the charismatic ants, bees and wasps, which attract the most general attention and include the social species, are all found in the Aculeata. There is a basal group of plant-eating sawflies (Symphyta), which includes several major pests, but the largest division by far is the Parasitica, containing perhaps a million species, the vast majority of which are parasitoids. Parasitoid larvae develop on or in the body of other animals, normally insects, eventually killing them. A single host provides all the resources that the developing larva needs to mature, and hence the parasitoid life cycle is somewhat intermediate between that of a predator and a true parasite (Godfray, 1994). The Parasitica contain a diverse array of insects, which are generally referred to as parasitoid wasps. Some of these are quite large in size, such as many ichneumon wasps, but there are many tiny species, often only a few millimetres in length, which are sometimes collectively referred to as microhymenoptera. *N. vitripennis* is one such insect, 2–3 mm long; it is a chalcid wasp, a member of the huge and diverse superfamily Chalcidoidea, which are characterized by a short antenna and highly reduced wing venation. The name chalcid comes from the Greek word for copper and the majority of chalcids, including *Nasonia*, have a metallic green colouration. The beauty of some chalcids has led to them sometimes being called jewel wasps.

Nasonia species are gregarious pupal endoparasitoids of cyclorrhaphan Diptera. In other words, the parent lays a clutch of eggs into the pupae of a group of fly species that are broadly related to the housefly (*Musca*). The larvae feed together inside the fly pupa (technically a puparia), where they form their own pupae, the adults emerging through little round holes drilled through the host puparial wall. A typical habitat in which to find *Nasonia* is in bird nests, where they attack flies that suck blood from young nestlings or feed on dead birds. The most well-known species is *N. vitripennis*, which is found in the northern hemispheres of both the Old and the

New World, but a further three closely related species (including one described for the first time in this issue) are found in bird nests in North America, where they specialize in *Protocalliphora* flies.

Houseflies and their relatives are straightforward, though smelly, to maintain in culture and hence entomologists interested in parasitoids quickly found *Nasonia* to be a useful model system to study in the laboratory. The first wave of research on *Nasonia* was in the 1940s–1960s (the genus was then called *Mormoniella*) and was largely genetical, making use of eye-colour mutants to study linkage and similar phenomena (Whiting, 1967). Like all Hymenoptera, *Nasonia* is haplodiploid (females are diploid and develop from fertilized eggs, whereas haploid male eggs are not fertilized), which simplifies some aspects of genotype scoring, an advantage that has again recently been exploited. Other early studies explored the mating behaviour of *Nasonia*, as well as its responses to different insecticides.

The second wave of *Nasonia* research began in around 1980 and was at least initially prompted by evolutionary rather than genetic questions. As *Nasonia* is haplodiploid, with sex determined by the fact of whether an egg is fertilized or not, natural selection can act on female behaviour to produce sex ratios that are adapted to local conditions. Indeed, when Hamilton (1967) formulated his theory of local mate competition, he listed a number of examples of species, including *N. vitripennis*, with high frequencies of sibmating and notably female-biased sex ratios to support his argument (Hamilton chose a picture of this wasp to adorn the front cover of the first volume of his collected papers). Sibmating frequencies are high in *Nasonia* because wasps from one brood emerge together and mate on the surface of the host puparium before dispersal. When sibmating is absolute, natural selection should favour the parent producing just enough sons reliably to fertilize all her daughters. However, when more than one family is involved (in the case of *Nasonia* because more than one wasp lay their eggs in the same hosts, or because the wasps from several hosts emerge in close proximity), a sex ratio intermediate between this and equality is favoured. Research, in particular by Werren and colleagues, has shown that females adjust their sex ratio as predicted by theory, which is one of the most impressive quantitative tests of sex allocation theory (Werren, 1980).

This work on *Nasonia* sex ratio also produced a series of surprises. Various strains produced highly biased sex ratios that were not predicted by theory, and research over the years has discovered a zoo of non-Mendelian inherited elements, each with its own optimum sex ratio. The first discovered element, *psr*, caused a male-biased sex ratio and is now known to be a B-chromosome that can be transmitted through sons but not daughters (Werren *et al.*, 1981). The nature of *msr*, which causes a female-biased sex ratio, is still not known, but it is preferentially transmitted through females (Skinner, 1982). Interestingly, models showed that in populations with local mate competition, *msr* can persist only in the presence of *psr* (Werren and Beukeboom, 1993). Another

strain also produced highly female-biased sex ratios and was initially called *sk* (for son killer) as males died in early development (Skinner, 1985). The causative agent turned out to be a maternally transmitted bacterium that was named, after the wasp, *Arsenophonus nasoniae* (Ghera *et al.*, 1991). The sequence of this bacterium is reported in companion papers to the *Nasonia* genome (Darby *et al.*, 2010; Wilkes *et al.*, 2010). By selectively killing males, the bacteria reduce within-host competition and hence increase the fitness of the females that will transmit *Arsenophonus*. Although non-Mendelian elements such as these are widespread, it is still remarkable to find so many in one species, and to be able to study how they interact.

There is yet another external element involved in the *Nasonia* story. It was discovered in the 1960s that there were mating barriers between some strains of *Nasonia*, and then in the 1980s it was shown that this was due to cytoplasmic incompatibility caused by the bacterium *Wolbachia* (Breeuwer and Werren, 1990). This microorganism is very widespread in insects and often spreads by disadvantaging uninfected females through modifying sperm in such a way that they can be used only by females carrying *Wolbachia*. The three closely related species of *Nasonia* carry incompatible *Wolbachia*, which acts as the main isolating mechanism. It also appears that the *psr* B-chromosome arose after a hybridization event between two closely related wasp species with different *Wolbachia* strains.

The latest phase of *Nasonia* research has seen the wasp emerge as a model system for speciation research and the present volume provides fine examples of this work. Once the *Wolbachia* have been removed, the three species can be crossed and the factors affecting hybrid fitness and the morphological differences between the species can be mapped. In this regard, the availability of the genome sequence will become increasingly useful and *Nasonia*'s haplodiploid genetics allows a more straightforward analysis of some traits than in full-diploid species. Speciation studies will benefit not only from the genome sequence of *N. vitripennis*, assembled using standard shotgun approaches, but also from the sequences of the siblings species, *N. giraulti* and *N. longicornis*, which were pyrosequenced and then assembled using the *N. vitripennis* sequence as a scaffold.

The genome sequence summary paper and some of the papers in this volume compare the *Nasonia* genomes with the increasing number of sequences now available, especially *Apis*, the honey bee, the most closely related existing sequence. The sequence also confirms the transfer of substantial stretches of *Wolbachia* genomes into the wasp (Hotopp *et al.*, 2007), which raises the interesting question of how they spread to fixation after the initial insertion. (I predict these stretches will code for the ability to use *Wolbachia*-modified sperm.) The sequence also identifies an ankyrin-repeat protein of a type previously known only from Pox viruses, but which now seem to be present in *Wolbachia*, their likely route into *Nasonia*. Parasitoid wasps locate their hosts using chemical cues, and inject a variety of venoms and other chemicals at oviposition to manipulate the host, and thus it is not surprising that odorant binding, gustatory receptor, odorant receptor and venom protein families are all well represented.

Already a range of genetic methodologies—from different array technologies through RNA interference

to single-nucleotide polymorphism and microsatellite libraries—are available or are under development for *Nasonia*. In addition to further studies on speciation, much of the rich biology of *Nasonia* that has been explored by evolutionary ecologists—sex ratio, clutch size, host finding and mating behaviour—will increasingly become amenable to genetic analysis. The completed genome sequence and the increasing importance of *Nasonia* is due to the work of many laboratories, but is also a personal triumph for Jack Werren of the University of Rochester, who has championed the work on this species for over 30 years. As someone who has spent much of his career studying parasitoids other than *Nasonia*, I fear this wasp is bent on world domination!

Conflict of interest

The author declares no conflict of interest.

HCJ Godfray

Department of Zoology, University of Oxford, Oxford, UK

E-mail: charles.godfray@zoo.ox.ac.uk

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