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My favourite nematode is *Phasmarhabditis hermaphrodita*, a parasite of terrestrial gastropods. So much so it has become the sole focus of my lab over the last few years. The reasons for this are fourfold. First, *P. hermaphrodita* is the only nematode to be developed as a weapon for slug and snail control. Research by David Glen and Mike Wilson et al. (with nematological expertise from David Hooper) in the late 80's and early 90's demonstrated that *P. hermaphrodita* can kill a selection of pestiferous slug species within 4-21 days (Wilson et al., 1993a); it could be grown en masse (Wilson et al., 1993b) and could provide protection against slug damage in mini-plot trials (Wilson et al., 1994) and in field trials (Wilson et al., 1995a) using many important agricultural, horticultural and floricultural crops (Rae et al., 2007). Further research focused on optimising mass production of this nematode and the influence that bacteria used as a food source could have on yield (Wilson et al., 1995b) and infectivity (Wilson et al., 1995c). *P. hermaphrodita* has been sold as Nemaslug® across Europe since 1994 and is routinely used by farmers and gardeners to control slugs. How is *P. hermaphrodita* able to kill slugs and snails? This is complicated but it has been suggested that *P. hermaphrodita* is like an entomopathogenic nematode, in that it vectors a bacterium (*Moraxella osloensis*) into slugs (Tan and Grewal, 2001), where it proliferates and causes septicaemia. Indeed it has been shown that high doses of *M. osloensis* injected directly into slugs will kill quickly and the purified lipopolysaccharide acts as an endotoxin (Tan and Grewal, 2002). However, this bacterium is not vertically transmitted and passed down to following generations and yet these nematodes, without *M. osloensis*, are still pathogenic (Rae et al., 2010). Therefore, the exact mode of action of *P. hermaphrodita* is still uncertain but the co-evolution of all these players including bacteria, nematodes and slugs warrants further attention.

Second, *P. hermaphrodita* has an interesting history and an exciting future. *P. hermaphrodita* was discovered in 1859 by Schneider and studied briefly by both

Maupas (1900) and Mengert (1953). However, what I find fascinating is that it could have easily been *C. elegans* a.k.a "the worm" as Sydney Brenner collected more strains of *P. hermaphrodita* than *C. elegans* in the early 1960's. Imagine a world where the discoveries of RNAi, the genetic regulation of apoptosis and the development of GFP (green fluorescent protein) that resulted in 3 Nobel prizes were due to studying the slug parasite *P. hermaphrodita* rather than *C. elegans*! Recently, *P. hermaphrodita* has been proposed as a model system of its own - specifically to study the evolution of parasitism (Wilson et al., 2015; Rae, 2017a; Andrus and Rae, 2018). Several attributes make it a perfect system and recently protocols have been developed that show how to culture it under lab conditions, mutagenize, mate and make isogenic lines of *P. hermaphrodita* just like *C. elegans* (Andrus and Rae, 2018). It is the only nematode from the 25,000 described species that has evolved to parasitise and kill slugs and snails. This is unusual as from the 108 nematode species associated with slugs and snails they are generally used as hosts for food, transport or to find a mate (Grewal et al., 2003). One of the fundamental questions in my lab is what are the genetic changes that lead to the emergence of parasitism? I think *P. hermaphrodita* is the perfect nematode to study this. As well as being able to be kept easily under lab conditions, it is in clade 9 and closely related to mammalian and insect parasites (van Megen et al., 2009). The ease of culture and collection, as well as the efforts of the 959 genome project will allow genomic comparison of *P. hermaphrodita* with not just *C. elegans* but many of the other fascinating rhabditid parasites that are free living, necromenic or phoretic as well as parasitic species. Although there is this potential for interesting discoveries, there is a severe lack of research into *P. hermaphrodita*. The majority of research is taxonomic or details the results of conducting surveys of slugs describing their associated nematode fauna with regular identification of *P. hermaphrodita* (or other *Phasmarhabditis* species) present. A noble endeavour but *Phasmarhabditis* warrants more than this approach. Specifically, what could these *P. hermaphrodita* isolates or *Phasmarhabditis* species tell us at the genetic level? By taking a natural variation approach, that has worked well in unravelling genes involved with traits such as phoretic behaviour (Lee et al., 2017) and social behaviour (de Bono and Bargmann, 1998) (to name but a few) in *C. elegans* and *Pristionchus pacificus* (see Sommer, 2015), the underlying genomic architecture of numerous genes involved with parasitism e.g. infection, pathogenicity or chemoattraction could be unravelled in *P. hermaphrodita.*

Third, *P. hermaphrodita* can manipulate the behaviour of slugs. Four hundred million years of co-evolution with terrestrial gastropods has created an arms race that at the present time has resulted in some striking effects that nematodes, specifically *P. hermaphrodita* can have on gastropods. Slugs infected with *P. hermaphrodita* are more likely to be found under refuge traps (Wilson et al., 1994), reduce feeding (Glen et al. 2000), move deeper down into soil to die (Pechova and Foltan, 2008) and move slower (Bailey et al., 2003). Whether these behaviours are because the slug is sick or the nematode is actively manipulating slug behaviour is unknown. Slugs will avoid areas where *P. hermaphrodita* is present (Wilson et al., 1999; Wynne et al., 2016) however, it has recently been shown that slugs infected with *P. hermaphrodita* are attracted to areas where *P. hermaphrodita* is present. This is presumably so more nematodes can infect and kill slugs and they can proliferate and mate faster (Morris et al., 2018). This study also showed (indirectly) that the potential mechanism of how these nematodes may control the slug's behaviour is by affecting serotonergic signalling, which is a similar method to other behaviour manipulating parasites (Hughes et al., 2012). The use of *P. hermaphrodita* has real potential to unravel the genetic mechanism of how parasites change the behaviour of hosts, which could be applied to other parasite/host systems.

Fourth, co-evolution of nematodes and gastropods has produced some fascinating abilities in the immune system of gastropods to provide protection against nematodes such as *P. hermaphrodita*. To date, the susceptibility of 19 slug species and 18 snail species have been tested by exposure to *P. hermaphrodita* under laboratory conditions (see Rae, 2017a for a complete description of gastropod species tested). Twelve slug species and eight snail species can be killed by *P. hermaphrodita* but it is unknown why some species are resistant to high doses of *P. hermaphrodita*. There is little information on the immune system of gastropods in general and specifically to do with infection by *P. hermaphrodita*. However, recent research has shown that the difference between slug and snail susceptibility is potentially due to an intriguing ability that the snail's shell possesses. Snails such as *Achatina fulica* (Williams and Rae, 2015) and *Cepaea nemoralis* (Williams and Rae, 2016) can actively trap, encase and kill nematodes using their shell. This whole process is remarkably efficient at killing nematodes, often hundreds at a time and is evolutionary conserved across the phylogeny of the Stylommatophora (terrestrial slugs and snails) (Rae, 2017b). An exciting opportunity has indirectly arisen from this research that may allow us to actually track the evolution of nematodes at the molecular level over time. Snail shells that are hundreds of years old present in museums have been shown to have nematode encased in their shells (Rae, 2017b, 2018). As nematode DNA can be extracted from shells this may facilitate genomic analysis over time using these preserved ‘fossilised’ specimens.

Here I hope I have outlined why *P. hermaphrodita* is a nematode that is worth studying. Unlike current model nematodes, it can be used to answer a suite of evolutionary questions about parasitism. Protocols are now in place detailing how to maintain *P. hermaphrodita* (Andrus and Rae, 2018) and the genome is currently being sequenced. New species are being discovered regularly, as well as strains of *P. hermaphrodita*, and the combination of using genomics and these natural strains could unravel how this biocontrol agent evolved to kill slugs and how this information could be translated to other species of nematodes or other organisms.

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