



Parasitoid fly induces manipulative grave-digging behaviour differentially across its bumblebee hosts



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Alterations of host behaviour in response to parasitism are widely documented. Modified host behaviour is considered an adaptive manipulation when it is induced by and provides a clear benefit to the parasite. Variability in the response of host organisms to parasitic manipulations can result in some hosts being more suitable than others if failure to induce a behaviour has fitness costs for the parasite. Individuals of the European bumblebee *Bombus terrestris* (Hymenoptera, Apidae) that are parasitized by the endoparasitic larvae of a conopid fly (Conopidae, Diptera) bury themselves in soil just before death. This behaviour, which is of little consequence to the dying host, improves the survival and fitness of the parasitoid. In this study, we examined whether a parasitoid conopid fly, *Physocephala tibialis*, can successfully induce self-burial or 'grave-digging' behaviour in three bumblebee host species (*B. bimaculatus*, *B. griseocollis* and *B. impatiens*). Self-burial behaviour was expressed in all three host species, but at a far lower rate (17.4%) in *B. griseocollis* than in the other two species, which showed nearly equal rates of self-burial when parasitized (~70%). *Bombus impatiens* and *B. bimaculatus* are more closely related to each other than to *B. griseocollis*, suggesting that genetic relatedness may influence host responsiveness to the parasitoid. We also found that larger hosts produced larger fly pupae, and that larger pupae generated bigger adult flies. In parasitoid literature, host suitability is often discussed in the context of receptiveness to oviposition and physiological resistance to infection. We posit that the ability to induce an important behavioural response influences host competency as well, and that host susceptibility to behavioural manipulation could have implications for selection.

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Parasites and parasitoids can alter host behaviour to increase their own fitness. Such adaptive manipulations (Poulin, 1995) may facilitate the transmission of the parasite between hosts (e.g. Baldauf et al., 2007; Carney, 1969; Perrot-Minnot, Kaldonski, & Cézilly, 2007) or promote survival of the parasite within its current host (e.g. Brodeur & McNeil, 1990; Khudr, Oldekop, Shuker, & Preziosi, 2013; Muller, 1994). For example, aphids parasitized by the braconid wasp *Aphidius nigripes* will leave their colonies and move to concealed microhabitats, protecting the wasp larvae it harbours from predation, hyperparasitism, and inclement weather (Brodeur & McNeil, 1989, 1990, 1992). Some parasites even induce their hosts to engage in beneficial defensive or 'body-guarding' behaviours after they have exited the host (reviewed in Maure, Daoust, Brodeur, Mitta, & Thomas, 2013).

When genetic variation of the parasite generates variance in host behavioural response (e.g. Khudr et al., 2013), the host

response then forms an extended phenotype of the parasite subject to selection (Dawkins, 1982; Hughes, 2012). Selection can favour host resistance to parasitism (reviewed in Moore, 1995), such as behavioural anapyrexia (seeking out cooler temperatures; e.g. Muller & Schmid-Hempel, 1993; Zbikowska & Cichy, 2012) and consumption of toxic substrates (e.g. Singer, Mace, & Bernays, 2009; Smilanich, Mason, Sprung, Chase, & Singer, 2011) that eliminate or retard the development of the parasite and/or prolong the life of the host, or selection can favour increased host manipulation by parasites (Van Houte, Ros, & Van Oers, 2013). In cases where induced behaviours favour the parasite without directly affecting host fitness, such as influencing where the host dies (e.g. Hughes et al., 2011; Muller, 1994), there may be strong selection on the parasite to manipulate the host but limited selection on the host to resist manipulation. Such selection could lead to specialization by the parasite if different host species express different behaviours when parasitized.

At present, few studies have examined the extent to which related hosts show species-specific behavioural responses to a shared parasite. Moore and Gotelli (1996) found that the behavioural responses of seven cockroaches to experimental infections

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with the same acanthocephalan parasite varied nonphylogenetically among cockroaches (i.e. closely related taxa responded differently). Similarly, Bauer, Grégoire, Bollache, and Cézilly (2000) found that sympatric congeneric species of amphipod, one native and one introduced, responded differently to infection with the same parasite, with only the native becoming attracted to light following infection. Korenko and Pekár (2011) determined that a polysphinctine wasp induced analogous but different behaviours (dense web spinning versus cupula production) in two theridiid spider hosts; in each host species, the wasp induced an innate overwintering web-building behaviour at an abnormal time that protected the parasite's offspring. In contrast, Korenko, Isaia, Satrapová, and Pekár (2014) found that two genera of polysphinctine wasp induced the same web-building behaviours in multiple species of congeneric orb-weaving spider hosts; although the induced behaviour differed depending on the identity of the infecting wasp, each wasp generated the same behavioural response across host species. Thus, across these studies, there is evidence for some induced behaviours remaining consistent across genera of hosts and others varying between closely related species. As the overall pattern of behavioural induction across potential hosts becomes better described, further research into the neurological (Liebersat, Delgado, & Gal, 2009) and genetic pathways of induction (Lefèvre et al., 2009; Tain, Perrot-Minnot, & Cézilly, 2007) may show that some types of adaptive manipulation, namely those of large effect across a narrow set of hosts, could lead to increased specialization. On the other hand, adaptive manipulations could maintain or even broaden host use if the parasite targets behavioural pathways governed by genes that are evolutionarily conserved across taxa, such as genes involved in insect locomotion (Van Houte et al., 2013).

Evidence from one study indicates that the endoparasitic larvae of conopid flies (Conopidae) carry out adaptive manipulations of their bumblebee (*Bombus* spp.) hosts. Muller (1994) showed that when *Bombus terrestris*, a European bumblebee species, is infected with the conopid *Physocephala rufipes*, the bee digs itself into the ground just before dying. Muller (1994) found that buried pupae were less susceptible to predation than those at the soil surface, indicating that burial improves conopid survival. Adult flies that emerged from buried pupae were also larger and heavier, both traits associated with increased adult fitness in parasitoids (Sagarra, Vincent, & Stewart, 2001; Visser, 1994; reviewed in Roitberg, Vincent, & Stewart, 2001), and had significantly fewer wing deformities than flies emerging from pupae at the ground surface (Muller, 1994). Although this phenomenon has been studied in only one species of bumblebee and one species of conopid fly, it may be widespread. Conopid flies are obligate, solitary endoparasitoids of insects, with four conopid genera commonly associated with bumblebees (Schmid-Hempel, 2001). This association extends across much of the geographical range of bumblebees, including North America (Freeman, 1966), Europe (Schmid-Hempel & Durrer, 1991) and Asia (Maeta & MacFarlane, 1993). Because the conopid pupa overwinters within the abdomen of the exoskeleton of its host bee and emerges as an adult fly the following spring (Skevington, Thompson, & Camras, 2010), selection should favour conopids that cause their primary host species to die in safe overwintering locations.

To date, Muller's study (1994) is the sole examination of self-burial as a behavioural response to conopid parasitism in bumblebees, despite extensive interactions between numerous species of conopids and bumblebees across wide geographical ranges. Here, we examine whether a conopid species, *Physocephala tibialis*, common in northern Virginia, U.S.A., induces digging behaviour in three locally common bumblebee species: *Bombus impatiens*, *B. bimaculatus* and *B. griseocollis*. The three bumblebee species

come from two subgenera (*Pyrobombus*, *Cullumanobombus*), permitting a comparison of the similarity of behavioural induction between closely related versus more distantly related hosts. In addition to behavioural induction, we compare measures of parasite performance among the three bumblebee hosts.

METHODS

Study Site and Bumblebee Collections

This study took place in 2012 from 11 June to 17 July at the University of Virginia's Blandy Experimental Farm (39°03'50.43"N, 78°03'47.20"W), a 283 ha field station located in the northern Shenandoah Valley of Virginia (Boyce, VA, U.S.A.). Each week for 6 weeks, we collected workers of the three most locally abundant bumblebee species (*B. bimaculatus* Cresson, *B. griseocollis* DeGeer, and *B. impatiens* Cresson) from flowers in early successional fields. We limited our collections to these three species, all of which are regionally common. Previous research indicates that conopids infect all three species in this region, with infection rates previously recorded as high as 35% of bees sampled from wild populations during the peak weeks of parasitism in late June and early July (Malfi & Roulston, 2014). Collections were conducted in clear weather during peak foraging hours (0800–1200 hours) 2–3 days per week. Each week, up to 30 female worker bees per target species were collected. During the first collection each week, bees were sampled at random from a variety of mass-flowering resources. Subsequent collections were targeted at particular bumblebee species with the goal of obtaining equal sample sizes of each species in a given week. Balancing sample sizes for each species was not always achieved because of phenological differences among the three species: *Bombus bimaculatus*, *B. griseocollis* and *B. impatiens* have annual life cycles that terminate in early, mid and late summer, respectively (Colla & Dumesht, 2010). After the fourth week of the study, the abundance of the early-season *B. bimaculatus* decreased substantially, but sample sizes of *B. griseocollis* and *B. impatiens* workers remained roughly equal throughout the study period.

Assessing Parasitism Status and Location at Death

Bees were placed into clear plastic tanks with 15 cm of loose topsoil covered with a thin layer of fallen leaves, sticks and rocks, following the design described by Muller (1994). Each tank measured approximately 46 × 32 × 34 cm and contained up to 20 bees of mixed species. Tanks were stored inside under dim lighting and kept at a temperature of 20–23 °C to provide comfortable conditions for the captive bees. Bees were fed a 1:2 sugar water solution ad libitum. If bees died on the surface of the soil, their bodies were pulled out and examined for the presence of conopid larvae/pupae as soon as possible. Otherwise, bee bodies were not recovered until all of the bees in a tank had died. At this time, the final (death) location of each bee was assessed. Each bee was classified as (1) a 'surface' bee if its body was on the surface of the leaf litter, on the surface of the soil, or on the surface of the soil and under the leaf litter, or (2) a 'buried' bee if it was buried in soil. To retrieve buried bees, dirt was gently scraped from the tanks manually and passed through a 4 mm wide-mesh sieve. When a bee was discovered in the soil, the depth of burial from the soil surface was estimated to the nearest centimetre. This was done by using a permanent marker to mark the level of the soil surface on the side of the tank prior to removal of soil. When a bee was found, a ruler was used to approximate the distance between the bee and the surface mark. In some cases, burial depth could not be recorded because bees were found upon resieving the soil from a tank.

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