



Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: [www.elsevier.com/locate/actoec](http://www.elsevier.com/locate/actoec)

## Figs, pollinators, and parasites: A longitudinal study of the effects of nematode infection on fig wasp fitness

Justin Van Goor, Finn Piatscheck, Derek D. Houston, John D. Nason\*

Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA

## ARTICLE INFO

## Keywords:

*Ficus*  
*Pegoscopus*  
*Parasitodiplogaster*  
 Dispersal  
 Longevity  
 Antagonism

## ABSTRACT

Mutualisms are interactions between two species in which the fitnesses of both symbionts benefit from the relationship. Although examples of mutualism are ubiquitous in nature, the ecology, evolution, and stability of mutualism has rarely been studied in the broader, multi-species community context in which they occur. The pollination mutualism between figs and fig wasps provides an excellent model system for investigating interactions between obligate mutualists and antagonists. Compared to the community of non-pollinating fig wasps that develop within fig inflorescences at the expense of fig seeds and pollinators, consequences of interactions between female pollinating wasps and their host-specialist nematode parasites is much less well understood. Here we focus on a tri-partite system comprised of a fig (*Ficus petiolaris*), pollinating wasp (*Pegoscopus* sp.), and nematode (*Parasitodiplogaster* sp.), investigating geographical variation in the incidence of attack and mechanisms through which nematodes may limit the fitness of their wasp hosts at successive life history stages. Observational data reveals that nematodes are ubiquitous across their host range in Baja California, Mexico; that the incidence of nematode infection varies across seasons within- and between locations, and that infected pollinators are sometimes associated with fitness declines through reduced offspring production. We find that moderate levels of infection (1–9 juvenile nematodes per host) are well tolerated by pollinator wasps whereas higher infection levels ( $\geq 10$  nematodes per host) are correlated with a significant reduction in wasp lifespan and dispersal success. This overexploitation, however, is estimated to occur in only 2.8% of wasps in each generation. The result that nematode infection appears to be largely benign – and the unexpected finding that nematodes frequently infect non-pollinating wasps – highlight gaps in our knowledge of pollinator-*Parasitodiplogaster* interactions and suggest previously unappreciated ways in which this nematode may influence fig and pollinator fitness, mutualism persistence, and non-pollinator community dynamics.

### 1. Introduction

Mutualistic interactions that benefit partner organisms are ubiquitous in nature and are associated with many ecological processes that underlie ecosystem function. Much is understood regarding the formation (Axelrod and Hamilton, 1981; Leung and Poulin, 2008) and regulation (Herre et al., 1999; Lee, 2015) of mutualistic associations over evolutionary time. Likewise, a broad range of mutualistic lifestyles, including context-dependent mutualisms and “cheater” partnerships, have been explored (Bronstein, 2001; Holland et al., 2004; Thompson and Fernandez, 2006), and many theoretical (Soberon and Martinez del Rio, 1985; Ferriere et al., 2001) and empirical (Boucher, 1982; Margulis and Fester, 1991; Maynard-Smith and Szathmary, 1995; Heil and McKey, 2003) studies of mutualism have focused on the fitness and stability of pairwise species interactions. Virtually all mutualistic species pairs, however, are members of more complex communities and

networks of organismal interactions. This context too can be important for a clear understanding of the ecological and evolutionary dynamics of mutualistic systems (Herrera et al., 2002; Thomson, 2003).

Mutualisms are almost universally targets for exploiter species that benefit from the products of mutualistic interactions but do not offer any benefits in return (Bronstein, 2001). Multiple species can antagonize a given mutualistic partnership through a variety of ecological roles, including predation, parasitism, or competition, and are likely to have profound effects on the stability of mutualistic partnerships. Over time, antagonists may coexist with their mutualist symbionts, destabilize mutualism through over-exploitation and drive the extinction of one or both mutualists, or enhance the stability of mutualism by aligning the fitness interests of mutualist partners. These concepts have been explored theoretically with contrasting results. Depending on model assumptions, antagonists have been found to influence mutualist and mutualist-antagonist stability negatively in some cases (Ferriere

\* Corresponding author.

E-mail addresses: [jvangoor@iastate.edu](mailto:jvangoor@iastate.edu) (J. Van Goor), [finnp@iastate.edu](mailto:finnp@iastate.edu) (F. Piatscheck), [derek.d.houston@gmail.com](mailto:derek.d.houston@gmail.com) (D.D. Houston), [jnason@iastate.edu](mailto:jnason@iastate.edu) (J.D. Nason).<https://doi.org/10.1016/j.actao.2018.03.007>Received 9 February 2017; Received in revised form 7 March 2018; Accepted 12 March 2018  
1146-609X/ Published by Elsevier Masson SAS.

et al., 2001; Mougi and Kondoh, 2014) or positively in others (Morris et al., 2003; Jones et al., 2009; Lee, 2015). Similarly, models have found the effect of antagonism on mutualism fitness to be negative (Sakata, 1994; Stanton et al., 1999), positive (Klinkhamer and de Jong, 1993; Maloof and Inouye, 2000), or neutral (Arizmendi et al., 1996; Bronstein, 2001). In contrast to theoretical studies, empirical studies of exploiter effects on mutualism have been relatively few (West and Herre, 1994; Thompson and Fernandez, 2006; Althoff, 2008; Mushegian and Ebert, 2015; Duthie and Nason, 2016). One impediment to investigating the effects of antagonism on mutualism fitness is that lifetime fitness in many systems is difficult to quantify (West et al., 1996; Bronstein, 2001). This impediment can be alleviated by focusing on model systems in which all strongly interacting species are known, ecological roles as mutualists and exploiters are well understood, and key components of lifetime fitness are easily estimated.

One such model system useful for addressing the effects of antagonists on the fitness of mutualists is the fig-fig wasp pollination-nursery mutualism. Figs (family Moraceae, genus *Ficus*) are represented by more than 750 species worldwide, with approximately 120 species in the New World (Berg, 1989). Figs are important components of tropical and subtropical ecosystems because their aseasonal fruit production serves as keystone food resource for a diversity of animal consumers (Terborgh, 1986; Lambert and Marshall, 1991; Shanahan et al., 2001). Figs are entirely reliant on typically host species-specific fig wasps (superfamily Chalcidoidea, family Agaonidae) for the pollination of fig inflorescences, while the pollinator wasp larvae develop within a subset of the fig female ovules (Janzen, 1979). This interaction is one of the most extensively examined and well-understood examples of mutualism, and has been the focus of many studies investigating ecological and evolutionary processes (Herre, 1989; Jusselin et al., 2003; Molbo et al., 2003; Jandér and Herre, 2010; Cruaud et al., 2012; McLeish and Van Noort, 2012). Associated with each fig-pollinator species pair is a number of typically host-specific (but see Marussich and Machado, 2007; Farrache current volume) non-pollinating wasps (superfamily Chalcidoidea, multiple families) that exploit the mutualism as parasites of developing wasps, ovule-gallers, and less frequently fig-wall gallers (Compton and Hawkins, 1992; Weiblen, 2002; Cook and Rasplus, 2003; Borges, 2015). Figs and their associates thus provide an excellent system for testing hypotheses concerning the influence of antagonists on mutualism fitness and stability.

To date, the vast majority of research investigating antagonist effects on the fig-fig pollinator mutualism has focused on non-pollinating fig wasps (West and Herre, 1994; West et al., 1996; Elias et al., 2012; Duthie and Nason, 2016). Equally ubiquitous, but much less studied, are entomopathogenic nematodes that parasitize fig pollinators (Martin et al., 1973). Nematodes of the genus *Parasitodiplogaster* (family Diplogastridae) are pan tropical parasites that specialize on fig wasp pollinators. These nematodes have been investigated in terms of morphology and taxonomy (Poinar, 1979; Poinar and Herre, 1991; Giblin-Davis et al., 2006; Kanzaki et al., 2016), infection rates (Giblin-Davis et al., 1995; Jauharlina et al., 2012), and virulence evolution based on pollinator population dynamics (Herre 1993, 1995). Research on Barro Colorado Island, Panama, indicates that *Parasitodiplogaster* infection reduces offspring production in most, but not all, fig pollinator species (Herre 1993, 1995).

To gain a deeper understanding of the impacts of *Parasitodiplogaster* on the fitness and stability of the fig-pollinator mutualism, we investigate inter-site variation in nematode-pollinator interactions, the effects of non-pollinating fig wasps on these interactions, and the fitness impacts of nematode infection at all stages in the pollinator life cycle. Specifically, this paper evaluates the mutualism consequences of inter-specific interactions between *Parasitodiplogaster* nematodes and wasp pollinators (genus *Pegoscapus*) associated with the Sonoran Desert rock fig, *Ficus petiolaris*. We determine how pollinator offspring production is influenced by nematode infection in the context of non-pollinator wasp antagonists across nine locations in Baja California,

Mexico. We also analyze the effects of nematode infection on the longevity of female pollinator wasps that have exited their natal fig. Further, we investigate the impacts of nematode infection on the dispersal ability of pollinator wasps searching for new, receptive figs. The results of these analyses are considered with respect to the fitness of the *Pegoscapus* pollinator and, more generally, of its mutualism with *F. petiolaris*. Unexpectedly, we observed nematodes infecting male pollinators and males and females of several non-pollinator wasp species, the implications of which we also consider with respect to fig-fig wasp population dynamics and mutualism stability.

## 2. Materials and methods

### 2.1. Background: figs, fig wasps, and *Parasitodiplogaster* nematodes

All *Ficus* are characterized by their production of a unique, nearly closed urn-shaped inflorescence commonly referred to as a fig. Neotropical *Ficus* are all monoecious and, depending on the species, their figs may contain tens to thousands of female and male flowers within the same enclosed inflorescence (Janzen, 1979; Herre, 1989). Figs containing receptive female flowers produce species-specific blends of volatiles (Chen et al., 2009; Wang et al., 2016) to attract pollen-bearing female pollinators, most of which are host-species specific. The successful pollinator enters the fig through a small terminal pore (the ostiole), pollinates the female flowers, and lays her eggs in a subset of these flowers before dying inside the fig. The foundress wasp thus initiates seed development for the plant and larval development for her own offspring, which gall the seeds in which they occur (Janzen, 1979). After approximately four to six weeks, seeds and larvae mature, and adult male wasps (unwinged) emerge from their galls to release and inseminate females. Females then collect pollen from male flowers while males chew an exit hole out of the fig. Prior to consumption of the mature fig by vertebrate frugivores (Shanahan et al., 2001), females exit via this hole to seek out new receptive figs in which to reproduce. Female pollinators have short adult lifecycles (< 60 h; Kjellberg et al., 1988; Dunn et al., 2008) but excellent dispersal capabilities, employing wind currents to reach receptive, host-specific *Ficus* trees that are often located many kilometers from their natal trees (Nason et al., 1998; Harrison and Rasplus, 2006; Ahmed et al., 2009).

Neotropical *Ficus* are subject to exploitation by a diversity of non-pollinating fig wasp genera (Bouček, 1993; West et al., 1996). Each fig typically supports at least one and often several non-pollinator species, most of which, like the pollinator, are host specific. The majority of non-pollinators are attracted to receptive figs by the same volatile blends produced to attract pollinators (Proffitt et al., 2007). They have also evolved life history characteristics similar to pollinating wasps in order to utilize resources within the developing fig, and to successfully time their emergence, mating, and departure from the mature fig. In contrast to the pollinator, which oviposits from inside the fig, all Neotropical (and most Old World) non-pollinators oviposit from the outside by inserting their ovipositors through the fig wall. Depending upon the species, non-pollinators parasitize developing ovules, pollinators, or non-pollinators, or induce galls within the fig wall. Thus, the non-pollinators may parasitize or be in direct or indirect competition for important components of the fig-pollinator mutualism (West and Herre, 1994; Weiblen, 2002; Jansen-González et al., 2014; Borges, 2015).

The life history of *Parasitodiplogaster* nematodes is tightly coupled with that of their fig pollinator hosts, which they rely upon for energy, transport to a new fig, and reproductive success. These nematodes are internal parasites that enter receptive figs inside the body of their host wasp, consume host tissue, mate (Fig. 1), and then disperse throughout the fig to reproduce (Giblin-Davis et al., 1995; Kanzaki et al., 2014; Ramirez-Benavides and Salazar-Figueroa, 2015). Nematode development is synchronized with fig and wasp development. Infective juvenile-stage nematodes are waiting inside the fig when pollinator females

Download English Version:

<https://daneshyari.com/en/article/8846492>

Download Persian Version:

<https://daneshyari.com/article/8846492>

[Daneshyari.com](https://daneshyari.com)