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Parasitism interacts with mutual interference to limit foraging efficiency in larvae of *Nephus includens* (Coleoptera: Coccinellidae)

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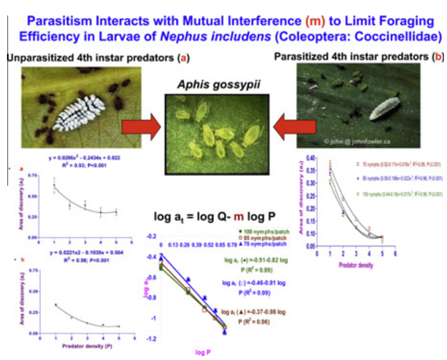
HIGHLIGHTS

- ▶ The effect of parasitism and predator–prey density on predator efficiency examined.
- ▶ Predation by predator larvae influenced by parasitism and mutual interference.
- ▶ The effect of parasitism and mutual interference declined as prey density increased.
- ▶ The invading predators may have higher impacts when they escape from parasitism.
- ▶ Carefully timed release of parasitism immuned-stages could maximize their control.

GRAPHICAL ABSTRACT



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ABSTRACT

Predator parasitism can modify predator–prey interactions through long-term (numerical) and short-term (functional response) impacts. However, mutual interference is another density-dependent factor that may affect predator foraging efficiency in the presence or absence of parasitism. This study examined the effects of parasitism of the invader *Nephus includens* (Kirsch) (Coleoptera: Coccinellidae) by *Homalotylus flaminius* Dalman (Hymenoptera: Encyrtidae), predator density, and prey density on the searching efficiency (a measure of area of discovery) using the cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) as alternate prey. Mutual interference reduced foraging efficiency by 47% in parasitized fourth-instar larvae compared to 44% in those unparasitized. Increasing predator density decreased searching efficiency more markedly in parasitized than in unparasitized larvae. The combined effects of parasitism and mutual interference reduced searching efficiency by 91%. Conversely, prey consumption by parasitized fourth-instar increased with increasing prey density, thus interference values declined from 0.98 to 0.82, indicating that the negative effect of parasitism on predator foraging diminished with increasing prey availability. Thus, these results support the inference of the 'enemy release' hypothesis, that invading predators may be more successful and have higher impacts on prey when they escape from parasitism. In the context of augmentation of *N. includens* in Egypt, releases of predator life stages immune to parasitism, by *H. flaminius*, (e.g., pupae or adults) in a suitable predator–prey ratio, especially early season, should minimize the detrimental effects of parasitism and intraspecific interference on foraging behavior, thus increasing predator ability to build up its population on alternative prey (aphid) and to attack later occurring target prey (mealybugs).

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1. Introduction

Invasive species can have profound impacts on invaded communities because they generate new trophic relationships, sometimes at the expense of autochthonous species. However, parasitism of the invasive species has the potential to attenuate these impacts (Dunn, 2009). Parasitism can drive changes in trophic interactions between other species and has the potential to alter broader community processes through long-term effects on densities of predators or their prey (Wilmers et al., 2006). There is also growing interest in short-term, 'trait-mediated indirect effects' of parasitism on predator–prey interactions (Hatcher et al., 2008). For example, parasitoid behavioral manipulation of hosts can lead to their increased vulnerability to predation (Lafferty, 1992; Shi et al., 2002; Dick et al., 2010).

The cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae), is a cosmopolitan plant pest of tropical, subtropical and warm temperate regions. It attacks hundreds of plant species and vectors at least 76 plant viruses (Chan et al., 1991). In Egypt, pesticides have been widely used for cotton aphid and mealybugs control in fruit and vegetable crops, especially guava, *Psidium guajava* L. (Abd El-Gawad and El-Zoghbey, 2009). However, the evolution of insecticide resistance and growing concerns of the environmental hazards of frequent insecticide applications have prompted more emphasis on biological control of aphids (van Emden and Harrington, 2007), especially the use of predators (Sarmento et al., 2007). For example, the predatory gall midge, *Aphidoletes aphidomyza* Rondani has been employed successfully for aphid control in cucumber culture (Bennison and Corless, 1993).

Coccinellid beetles are an important group of predatory insects with considerable biocontrol potential against aphids and other pest species (Hodek and Honěk, 1996; Michaud, 2012). They feed on a wide range of prey, tend to be very voracious, and can exhibit rapid numerical responses (Hodek and Honěk, 1996; Bayoumy, 2011). However, they do not always maintain prey populations in check (Northfield et al., 2010; Michaud, 2012). Thus, evaluations of particular aphidophagous species in specific agronomic situations are needed to assess their biological control potential. The lady beetle *Nephus includens* (Kirsch) (Coleoptera: Coccinellidae) is a primarily coccidophagous species of Palearctic origin and an effective predator of some agriculturally important mealybugs in Greece (Argyriou et al., 1976). It has fortuitously established in Egypt where it has been recently found preying on mealybugs (Abdel-Salam et al., 2010). *N. includens* has been studied as a predator of the citrus mealybug, *Planococcus citri* (Risso) and its biological performance on that species has been assessed in Italy (Tranfaglia and Viggiani, 1972). The life table parameters of *N. includens* also have been studied on other mealybug species (e.g., Canhilal et al., 2001; Al-Khateeb and Asslan, 2007; Abdel-Salam et al., 2010). Although alternative prey species have not been thoroughly catalogued for *N. includens*, it has been observed in Egypt feeding on the cotton aphid *A. gossypii* (Bayoumy, 2011). Thus, relatively little is yet known of this species' biology or ecology in Egypt.

The thelytoky parasitoid, *Homalotylus flaminius* Dalman (Hymenoptera: Encyrtidae) is a solitary, koinobiont endoparasitoid attacking the second-instar larvae of several species of coccinellids, including *N. includens* (Novin et al., 2000; Ma and Lin, 2001; Abdel-Salam et al., 2010). The genus Homalotylus comprises the most important parasitoids of Coccinellidae with about 50 species worldwide (Noyes, 2005). *Homalotylus sinensis* Xe and Hu has been reported as a larval parasitoid of *Nephus bipunctatus* (Kugelann) from Iran (Fallahzadeh et al., 2006). Up to 90–95% of larvae of the coccinellid *Chilocorus bipustulatus* L. have been parasitized by *H. flaminius* in North Africa and the Black Sea region (Rubtsov, 1954; Majerus, 1994). The foraging behavior and predatory efficiency of coccinellids may be affected by many factors including their developmental stage (Koch et al., 2003), body size (Kajita and Evans, 2010), the prey species (Sarmento et al., 2007), prey density (Matter et al., 2011), temperature (Skirvin et al., 1997), foraging cues (Hodek and Honěk, 1996; Pasteels, 2007), plant architecture (Grevstad and Klepetka, 1992), cannibalism and intraguild predation (Burgio et al., 2002), food deprivation (Santos-Cividanes et al., 2011), and entomopathogenic fungi (Poprawski et al., 1998). However, few studies have yet examined the potential impact of larval parasitism on coccinellid foraging behavior. Bayoumy (2011) assessed the effect of *H. flaminius* parasitism of *N. includens* larvae by deriving functional responses for parasitized second- and fourth-instars preying on *A. gossypii* at different prey densities. Although, parasitism did not alter the type of response in early-parasitized second-instar *N. includens*, it adversely affected the response of fourth instars, ostensibly due to the more advanced age of the parasitoid larva. Unparasitized fourth-instars were observed to be the most voracious stage with the highest attack rate and lowest handling time, and thus were selected for use in the current study.

One of the most informative methods for studying the predator–prey interaction involves measuring functional response and searching efficiency as these often correlate with biocontrol efficacy (Lester and Harmsen, 2002; Pervez and Omkar, 2005; Fathipour et al., 2006; Bayoumy, 2011). Various models have been proposed to describe the interactions of one prey with one predator, beginning with the Lotka–Volterra model (Lotka, 1925; Volterra, 1926). However, models for the interaction of more than two species, for example, predator–prey interactions with parasitism as an additional factor, have been less studied because more complex phenomena arise (Freedman and Waltman, 1985).

In many cases, parasitism modifies the external features of an organism or its behavior to render it more vulnerable to predation (e.g., Lafferty, 1992; Shi et al., 2002). Although parasitized animals often exhibit a reduction in food consumption (e.g., Arnott et al., 2000; Wright et al., 2006), parasitism may also trigger an increase in consumption (Slansky and Scriber, 1985; Dick et al., 2010). Thus, counterintuitively, parasitism might increase the competitive ability and/or functional response of invading predators. In the context of previous work on the invasive *N. includens*, (Bayoumy, 2011), here we compared the searching efficiency of parasitized and unparasitized individuals to infer likely consequences of parasitism for population and community processes. A secondary objective was to test whether intraspecific interference would interact with parasitism via effects on predator consumption rates. Specifically, this work aimed to investigate (1) the impact of parasitism by *H. flaminius* on the searching efficiency of fourth-instar *N. includens* and its interaction with predator density (i.e., mutual interference) and (2) the effect of various predator–prey density combinations on searching efficiency and mutual interference values for parasitized fourth-instar *N. includens*.

2. Materials and methods

2.1. Insect cultures and general experimental conditions

A colony of *N. includens* was established from pupae collected on guava trees, *Psidium guajava* L. at the experimental Farm, Faculty of Agriculture, Mansoura University at Mansoura district, Egypt during 2010-spring season. These trees were infested with *Icerya seychellarum* Westwood, *Planococcus citri* Risso and *A. gossypii*. Pupae ($n = 96$) were placed in Petri dishes (6.0 cm diameter × 2.0 cm height, $n = 6$/dish) lined with filter paper and transported to the laboratory. Pupae were maintained at

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