



The effect of obligate hyperparasitoids on biological control: Differential vulnerability of primary parasitoids to hyperparasitism can mitigate trophic cascades

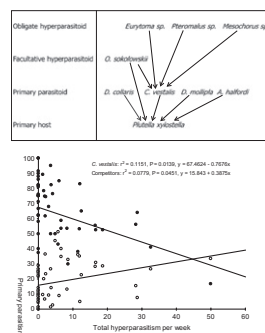
Robert S. Nofemela *

Insect Ecology Division, ARC-Plant Protection Research Institute, Private Bag X134, Queenswood 0121, South Africa
Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Pretoria 0028, South Africa

HIGHLIGHTS

- ▶ *Cotesia vestalis* was a dominant primary parasitoid of *Plutella xylostella*.
- ▶ It was also a secondary host to three obligate hyperparasitoid species.
- ▶ At low hyperparasitism, *C. vestalis* limited hosts available to competitors.
- ▶ As *C. vestalis* population declined, competitors parasitized more of available hosts.
- ▶ Species that are invulnerable to hyperparasitism took over role of the vulnerable.

GRAPHICAL ABSTRACT



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ABSTRACT

Obligate hyperparasitoids are widely considered an important ecological disturbance to biological control of insect pests, as they develop at the expense of primary parasitoids. However, supporting evidence is largely derived from direct trophic interactions in simple food webs. Yet, a multitude of insect pest populations simultaneously support development of several primary parasitoid species in horticultural and natural systems. Since primary parasitoid species in a community can differ in vulnerability to obligate hyperparasitoids, it is desirable to establish if the invulnerable primary parasitoids can take advantage of reduced competition from affected species by increasing their contribution to total primary parasitism levels thereby mitigating effects of hyperparasitism on biological control. To investigate this question, populations of the diamondback moth, *Plutella xylostella* (Linnaeus) (Plutellidae), its primary parasitoids and hyperparasitoids were monitored on unsprayed cabbage plots at weekly intervals over six consecutive years. *Cotesia vestalis* (Haliday) (Braconidae), a dominant primary parasitoid in this system, was a secondary host to three obligate hyperparasitoids: *Mesochorus* sp. (Ichneumonidae), *Eurytoma* sp. (Eurytomidae) and *Pteromalus* sp. (Pteromalidae). The higher efficiency of *C. vestalis* in utilizing younger host larvae at lower hyperparasitism levels limited host availability to other major primary parasitoids. But, as hyperparasitism levels increased and its populations declined, populations of *Oomyzus sokolowskii* (Kurdjumov) (Eulophidae) and *Diadromus collaris* (Gravenhorst) (Ichneumonidae) increased significantly as they parasitized a greater proportion of available hosts. As a consequence, the impact of hyperparasitoids did not result in trophic cascades, as their impact on total primary parasitism levels and infestation levels was insignificant. This study shows that primary parasitoid species that are invulnerable to hyperparasitism can take over the function of vulnerable ones in communities where interspecific interactions

* Corresponding author. Address: Insect Ecology Division, ARC-Plant Protection Research Institute, Private Bag X134, Queenswood 0121, South Africa. Fax: +27 12 329 3278.

E-mail address: NofemelaR@arc.agric.za

among species are strong. Thus, an approach that considers both direct and indirect effects of hyperparasitoids in primary parasitoid communities improves our understanding of the net impact of hyperparasitism on biological control of insect pests.

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1. Introduction

Biological control theory suggests that consumer species can effectively suppress their host or prey populations (Hairston et al., 1960; Crawley, 1989). However, the strong top-down effect of consumers not only influences the population size of prey/hosts, but can indirectly influence population densities of species in lower trophic levels. This propagation of strong effects of higher-order consumers through the food web is called a *trophic cascade* (Polis et al., 2000). In a simple food web involving a *host plant – an insect herbivore – a primary parasitoid*, high parasitism of the herbivore population benefits the host plant if infestation levels are reduced (Murdoch and Briggs, 1996; Hawkins and Cornell, 1999; Matsumoto et al., 2003). Although primary parasitoids are widely utilized for biological control of insect pests (DeBach and Rosen, 1991), they do not occupy the highest trophic level. Due to direct relevance of trophic cascades to biological control practice, the effect of secondary parasitoids (hereafter referred to as 'hyperparasitoids') on efficiency of primary parasitoids is an important topic in biological control (Rosen, 1981; Rosenheim, 1998; Sullivan and Völkl, 1999).

Four types of hyperparasitoids are described (Sullivan and Völkl, 1999; Walter and Abeeluck, 2006); but only two types (i.e., facultative and obligate) are found where Lepidoptera are plant pests (Sullivan and Völkl, 1999), which is a focus of this study. Facultative hyperparasitism is a form of omnivory, where a parasitoid feeds on two trophic levels by acting both as a primary parasitoid and a hyperparasitoid (Brodeur, 2000). However, this group of hyperparasitoids is not considered detrimental to biological control, except where they selectively parasitize primary parasitoids more than the insect pest population (Moore and Kfir, 1995; Pérez-Lachaud et al., 2004). In contrast, obligate hyperparasitoids only reproduce on primary parasitoids, and this direct impact on primary parasitoid populations has made them the most studied hyperparasitoid group (Clausen, 1972; Sullivan and Völkl, 1999). They are divided into two subcategories: (1) those attacking larvae of primary parasitoids through the body of insect pests and, (2) those attacking primary parasitoid pupae outside the body of insect pests (Sullivan and Völkl, 1999). The presence of both subcategories in a food web can alter the food web structure if those species attacking primary parasitoid pupae also parasitize species attacking larval stages (Carew and Sullivan, 1993; Brodeur, 2000).

A majority of studies have shown that presence of obligate hyperparasitoids increases herbivory as insect pest populations are often released from the strong top-down effect of primary parasitoids (Bourchier and Nealis, 1992; Eichhorn, 1996; Boenisch et al., 1997; Lei and Hanski, 1997; Rosenheim, 1998; Brodeur, 2000; Schooler et al., 2011). Further, obligate hyperparasitoids can leave cues on the plant surface that may increase dispersal probability of primary parasitoids, which further reduces mortality of insect pests (Höller et al., 1993; van Veen et al., 2001). However, other studies have shown that the impact of obligate hyperparasitoids is not always sufficiently large to result in trophic cascades (Cameron and Walker, 2002; Roltsch et al., 2006; Araj et al., 2009) due to: (1) the ability of some primary parasitoids to modify the behavior of parasitized hosts (Brodeur and McNeil, 1992; Tanaka and Ohsaki, 2006, 2009), (2) density-independent hyperparasitoid aggregation (Weseloh, 1986; Ayal and Green, 1993; Schooler et al., 1996; Müller and Godfray, 1998), and (3) lower reproductive

potential of obligate hyperparasitoids compared to their primary parasitoid hosts (Brodeur, 2000).

Although these studies provided important basic knowledge of differential impact of obligate hyperparasitoids on biological control of insect pests, they largely investigated this indirect effect using direct trophic interactions. Yet, a multitude of insect herbivore populations are known to simultaneously support development of several primary parasitoid species in natural and horticultural systems (Godfray, 1994; Hawkins, 1994; Müller et al., 1999). Although obligate hyperparasitoids are not host-specific, they do not just attack any primary parasitoid species as their host range is restricted by developmental traits of their hosts (Grasswitz and Reese, 1998; Chow and Mackauer, 1999; Schwarz and Shaw, 2000; Day, 2002). Thus, primary parasitoid species that perform the same function in a community (e.g., egg, larval or pupal parasitoids, and thus are functionally redundant; Loreau, 2004; Casula et al., 2006) may be equally vulnerable to obligate hyperparasitoids that require their shared traits (Clausen, 1972). However, primary parasitoids that attack different life stages of a common host population (i.e., they perform different functions in the community, and thus are functionally complementary; Wilson et al., 1999; Cardinale et al., 2003; Veddele et al., 2010) usually have different suites of hyperparasitoids. Thus, the developmental traits of primary parasitoid species in a community determine whether a given obligate hyperparasitoid produces species-level or community-level trophic cascades (see Polis et al., 2000; Schmitz et al., 2000).

The life stages of the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae), are attacked by several species of primary parasitoids in South Africa, of which *Cotesia vestalis* (Haliday) [= *Cotesia plutellae* (Kurdjumov)], a solitary koinobiont larval parasitoid, is the most dominant. However, its larval and pupal stages are in turn attacked by three species of obligate hyperparasitoids (Waladde et al., 2001; Mosiane et al., 2003; Smith, 2004; Nofemela and Kfir, 2005). In this study, I use long-term data sets to establish whether: (1) the effect of obligate hyperparasitoids on *C. vestalis* populations are significantly high to limit its impact on *P. xylostella*, (2) the invulnerable primary parasitoid species increase their contribution to total parasitism levels as populations of *C. vestalis* decline, and (3) the population increase of invulnerable primary parasitoids effectively counteracts the effect of hyperparasitoids on *C. vestalis*.

2. Materials and methods

2.1. Study area

The study reported here was conducted on a research farm belonging to the ARC-Institute for Industrial Crops at Brits (25° 59' S, 27° 76' E, altitude 1 082 m), North West Province of South Africa. The Brits municipality area is within the Highveld, i.e., a high plateau inland region characterized by temperate climate and summer rainfall (Rutherford et al., 2006). The study site is within the Marikana Thornveld, a component of the Savannah Biome, where dominant natural vegetation is *Acacia karroo*. The soil type is mainly vertic melanic clays with some dystrophic or mesotrophic plinthic catenas and some freely drained, deep soils. Long-term annual precipitation is between 600 and 700 mm, and

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