Available online at www.sciencedirect.com
ScienceDirect
Biological Control 46 (2008) 133–139
Biological Control
www.elsevier.com/locate/ybcon

Benefits of self-superparasitism in a polyembryonic parasitoid

Jennifer A. White [a,*], D.A. Andow [b]

[a] Department of Ecology, Evolution and Behavior, University of Minnesota, 100 Ecology, 1987 Upper Buford Circle, St. Paul, MN 55108, USA
[b] Entomology Department, University of Minnesota, 219 Hodson Hall, 1980 Folwell Avenue, St. Paul, MN 55108, USA

Received 28 September 2007; accepted 8 April 2008
Available online 14 April 2008

Abstract

Macrocentrus grandii is a polyembryonic parasitoid, with embryos that divide asexually within the host (European corn borer, *Ostrinia nubilalis*) to produce broods of clonal offspring. From a biological control standpoint, polyembryony seems advantageous because each parasitized host yields multiple parasitoids with minimal time and egg investment. When we observed *M. grandii* in the field, however, we found that the parasitoid virtually always invested additional time and, if possible, stings into hosts that it had already stung, apparently reducing some of the advantages of polyembryony. We therefore investigated and found support for two potential benefits that can be gained by self-superparasitism in this system. First, multiple stings allowed production of mixed-sex broods: 27% of multiply-stung versus 0% of singly-stung hosts produced mixed-sex broods. Second, multiple stings increased mean parasitoid progeny produced per host, primarily by reducing the chance of complete brood failure. Our results indicate substantial benefit for a second sting, but little benefit for three or more stings, even though *M. grandii* was sometimes observed to invest more than two stings within a single host. However, we also found that within-host larval competition is prevalent, suggesting that supernumerary stings may pay off in competition against conspecific larvae. Such additional investment within a single host would be particularly beneficial when hosts, rather than eggs, are limiting, but would decrease the overall efficacy of *M. grandii* as a biological control agent.

Keywords: Clutch size; Foraging behavior; Host utilization; Intraspecific competition; *Macrocentrus grandii*; *Ostrinia nubilalis*; Polyembryony; Self-superparasitism

1. Introduction

Concealed hosts such as the European corn borer (*Ostrinia nubilalis* Hübner [Lepidoptera: Crambidae]) have been difficult targets for biological control (Hawkins et al., 1993), in part because few natural enemies are well-adapted to exploiting the brief windows when European corn borer larvae are vulnerable to attack (White and Andow, 2007). Many parasitoids released against the European corn borer failed to establish (Baker et al., 1949), and few established species achieve noticeable levels of parasitism (e.g. Mason et al., 1994; Shanklin et al., 1998). One of the most successful, although still limited, parasitoids of the European corn borer is *Macrocentrus grandii* Goidanich (Hymenopetera: Braconidae; also known as *Macrocentrus gifuensis* Ashmead and *Macrocentrus cingulum* Brischke), which generally achieves low to moderate levels of parasitism (e.g. Onstad et al., 1991; Winnie and Chiang, 1982). One unusual aspect of *M. grandii*'s life history that may contribute to the relative success of this parasitoid is polyembryony.

Polyembryony is a developmental lifestyle in which embryos split during development to produce multiple offspring that are genetically identical to one another, but not to their mother (Craig et al., 1997). Polyembryony has evolved independently in a variety of animal taxa, including four lineages of parasitic hymenoptera, and has been suggested to be a particularly advantageous trait for organisms in which the offspring have more information regarding optimal clutch size than the parents (Craig et al., 1997).

* Corresponding author. Present address: Department of Entomology, University of Arizona, 410 Forbes Building, P.O. Box 210036, Tucson, AZ 85721-0036, USA. Fax: +1 520 621 1150.
E-mail address: jenwhite@email.arizona.edu (J.A. White).

1049-9644/$ - see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.biocontrol.2008.04.005

For *M. grandii*, polyembryony allows a female to efficiently make use of limited windows of European corn borer vulnerability, producing multiple offspring per host with minimal time and egg investment. Consequently, there would seem to be little reason for *M. grandii* to invest additional effort into a host, once it has been stung. Indeed, based on optimal foraging theory, one would predict that self-superparasitism in polyembryonic species should be discouraged evolutionarily as a waste of time and/or eggs (Stephens and Krebs, 1986; Rosenheim and Hongkam, 1996).

Despite these expectations, preliminary observations of *M. grandii* in the field indicated that this parasitoid does apparently self-superparasitize, as do a number of other polyembryonic species (Strand, 1989a,b; Hoffmeister et al., 2000; Zappalà and Hoy, 2004). In at least one case, the primary purpose of the additional egg appears to be production of mixed-sex broods. *Copidosoma floridanum* lays exactly one or two eggs per host: hosts that receive one egg produce unisexual broods, and the vast majority of hosts that receive two eggs produce mixed-sex broods (Strand, 1989b). Mixed-sex broods are advantageous in species capable of inbreeding, because local brother–sister matings upon emergence help to assure offspring reproductive success (Godfray, 1994). Production of mixed-sex broods requires deposition of only two eggs, however, and *M. grandii* has been reported to sting a restrained host as many as 20 times (Parker, 1931).

Of what possible advantage are these additional stings? Two possibilities were suggested by Parker (1931). He inferred that a single egg was only capable of producing 8–10 offspring, and that multiple ovipositions were therefore needed to fully utilize the host and produce broods that averaged 20 individuals. This conclusion, however, was highly speculative because it was based on a distribution of brood sizes that emerged from hosts where the underlying number of stings per host was unknown. When the number of stings was controlled (J. White, unpublished data; present study), we found that a single oviposition was sufficient to produce large broods capable of fully using the host.

An alternative possibility stems from Parker's observations. He dissected numerous recently-stung European corn borer larvae, and when he was able to find *M. grandii* eggs, they were located indiscriminately throughout the host's body, suggesting that some fraction of eggs may be laid in inappropriate places (e.g. the gut) and fail to produce any offspring at all. Other parasitoid species have been noted to have low rates of success per egg for this reason (Martin, 1914, as cited in Hoffmeister et al., 2000). In addition, eggs can be destroyed by host immune response (van Alphen and Visser, 1990), some proportion of stings may fail to result in egg deposition, and/or some proportion of eggs may be inviable. In any of these situations, multiple stings into the same host would be favored as insurance that progeny are produced, particularly if multiple stings depress the host's immune response, and/or the costs of additional stings are minimal.

The purpose of the present study was twofold. First, we confirmed the presence of multiple stings by *M. grandii* under field and laboratory conditions into unrestrained hosts, quantifying the cost to the parasitoid in terms of time and presumed egg investment. Second, we evaluated the potential benefit of multiple stings to the same host by manipulating the number of stings per host and quantifying progeny production.

2. Methods

2.1. Study system

The European corn borer feeds solitarily in concealed locations within the host plant and is only intermittently accessible to *M. grandii*, which cannot enter corn borer tunnels or penetrate plant material with its ovipositor (White and Andow, 2007). *M. grandii* is attracted to volatile chemicals associated with corn borer feeding (Ding et al., 1989; Udayagiri and Jones, 1992), but due to the inaccessibility of the host, the proportion of these patch visits that result in successful oviposition for the parasitoid is relatively low. We have defined a "sting" within this system as ovipositor contact with a host, followed by a distinctive cocking behavior (Parker, 1931), similar to that described for *Venturia canescens* (Rogers, 1972). Note that while a sting likely coincides with an oviposition, the two are not necessarily equivalent. We have found that the ovipositor cocking behavior is a necessary indicator of oviposition (we never observed parasitoid progeny when the cocking behavior was absent; J. White, unpublished data), but cannot absolutely verify that it is a sufficient indicator of egg deposition. *M. grandii* eggs are very small and deposited indiscriminately within the much larger host (Parker, 1931), so dissecting the host to quantify parasitoid eggs is not feasible. We therefore have restricted our study to an interpretation of stinging behavior, with the explicit realization that some stings may not have resulted in ovipositions. If lack of oviposition were the driving factor in multiple stings, then an interpretation of "self-superparasitism" would clearly be unwarranted. However, the results of our study are highly suggestive that additional post-sting investment into the host is not driven by failed ovipositions, support the supposition that a sting coincides with an oviposition, and indicate that most, if not all, multiple stings are multiple ovipositions, and therefore self-superparasitism.

2.2. Post-sting investment by *M. grandii*

We evaluated post-sting time investment and self-superparasitism by *M. grandii* in both the field and in the laboratory. All wasps used in these experiments either originated from wild-collected broods or were laboratory-propagated for no more than two generations, to minimize the selective influence of laboratory conditions on wasp behavior. Prior to experimental use, wasps were main-