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Facultative hyperparasitism by the potential biological control agent *Aptesis nigrocincta* (Hymenoptera: Ichneumonidae)

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Abstract. This study investigated whether *Lathrolestes ensator*, a parasitoid released as a biological control agent against the European apple sawfly in Canada, is successfully attacked by the cocoon parasitoid *A. nigrocincta*. In a no-choice situation in the laboratory, there was no significant difference between the acceptance of unparasitized hosts and hosts containing an egg of *L. ensator* by females of *A. nigrocincta*. In addition, *A. nigrocincta* attacked mature larvae of the larval parasitoid to the same degree as they attacked unparasitized hosts. Survival of *A. nigrocincta* offspring was close to 100% regardless of whether they developed in unparasitized hosts, in hosts containing an egg of *L. ensator* or in host cocoons containing mature larvae of *L. ensator*. This is discussed in the context of the possibility of releasing *A. nigrocincta* as an additional biological control agent of the European apple sawfly.

INTRODUCTION

The European apple sawfly, *Hoplocampa testudinea* Klug (Hymenoptera: Tenthredinidae) is univoltine and a primary pest of apple orchards feeding exclusively on apple fruitlets. Introduced from Europe into Long Island, New York, in 1939, *H. testudinea* was discovered for the first time in southern Quebec, Canada in 1979 (Paradis, 1980) and later spread throughout all the apple-growing areas of this province (Vincent & Mailloux, 1988). A survey conducted in Central Europe looking for potential candidates that might be used in a classical biological control programme of apple sawfly revealed two parasitoids of importance (Cross et al., 1999). *Lathrolestes ensator* Brauns (Hymenoptera: Ichneumonidae) is a solitary koinobiotic endoparasitoid known only to attack the European apple sawfly (Cross et al., 1999). It attacks early instar larvae and remains in the egg stage until the host has dropped to the ground and built its cocoon. During July and August, the parasitoid larva consumes the host and by the end of September has reached the prepupal stage and constructed a flimsy cocoon against the inner walls of the host cocoon (Zijp & Blommers, 1993). The other parasitoid of importance found in this survey, *Aptesis nigrocincta* Gravenhorst (Hymenoptera: Ichneumonidae), attacks the hosts below ground. In order to reach the host, females first have to penetrate the tough cocoon built by the mature sawfly larva. The host range of *A. nigrocincta* is not well known but it appears to be oligophagous attacking several sawflies (Cross et al., 1999). This solitary idiobiotic ectoparasitoid completes two generations each year (Babendreier, 1999). During the first generation female *A. nigrocincta* encounter cocoons containing either unparasitized hosts or hosts containing one or more eggs of the larval parasitoid *L. ensator*, whereas females of the second generation encounter cocoons containing either unparasitized hosts or mature larvae or prepupae of *L. ensator*.

Since *L. ensator* is host specific on European apple sawfly, it was decided to introduce this larval parasitoid into Canada and the first recoveries occurred in release orchards recently (Vincent et al., 2001). The cocoon parasitoid *A. nigrocincta*, however, was found to have considerable impact on apple sawfly populations (Babendreier, 2000) and thus is regarded as a potential additional biological control agent. The selection of appropriate agents is of critical importance for biological control (Waage, 1990). In particular, interspecific competition can be a key factor influencing both the structure of a parasitoid complex and the dynamics of host-parasitoid interactions (Pschorn-Walcher, 1985; Viggiani, 1994; Mills & Gutierrez, 1996) and thus investigation of competition between potential agents is of primary importance in biological control programmes (Pschorn-Walcher & Zwölfer, 1968; Mills, 1994). Specialised parasitoids attacking early host stages may suffer severely from later attacking competitors (e.g. Pschorn-Walcher, 1967) and the success of biological control introductions against a particular pest species may be largely dependent on such competitive relationships (e.g. Syme, 1981; see also Waage & Mills, 1992). The aim of the present study was to investigate whether hosts containing different stages of the primary parasitoid, *L. ensator*, are successfully attacked by the cocoon parasitoid *A. nigrocincta*.

MATERIAL AND METHODS

Culture of hosts and parasitoids

Unparasitized hosts as well as hosts parasitized by the larval parasitoid *L. ensator* were obtained from collections of apples infested by late instars of the European apple sawfly in commercial apple orchards in Switzerland and Germany in June 1997. Apples were placed on wire screens, that were suspended over plastic trays to receive the descending sawfly larvae. Larvae were removed twice a day and checked for parasitism by *L. ensator* under a microscope (magnification 25×, the black parasitoid eggs were easily visible through the integument of the sawfly larvae). Unparasitized and parasitized host larvae were separated and allowed to burrow into soil in plastic cylinders (1.3 l) where they formed cocoons. For the experiments only those hosts containing a single parasitoid egg were used. All host cocoons were stored under near outdoor conditions in an insectary. One day prior to the experiments cocoons were sieved out of the soil and stored at 20°C. *A. nigrocincta* was obtained from collections of apple sawfly cocoons from an organically managed apple orchard in north-eastern Switzerland in 1996. Emerging parasitoids were identified and a culture was estab-

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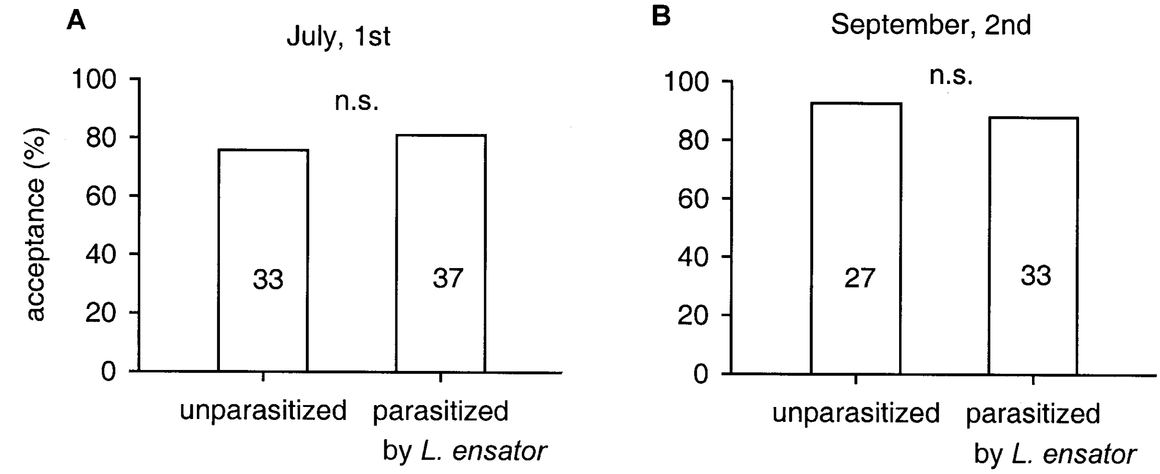

Fig. 1. Acceptance (= oviposition) by *Aptesis nigrocincta* females of either unparasitized cocoons of the host, *Hoplocampa testudinea,* or of host cocoons parasitized by the larval parasitoid, *Lathrolestes ensator*. Parasitized cocoons either contained an egg of *L. ensator* (A) or a mature larva of *L. ensator* (B). Number of females tested is indicated inside the bars.

lished on apple sawfly cocoons and maintained in the laboratory. All female parasitoids used for experiments were kept singly in Petri dishes (94 mm) at 20°C and provided with honey and water ad libitum.

Experimental design

We investigated the oviposition behaviour of *A. nigrocincta* females on host cocoons that either contained a single egg (1st July 1997, experiment 1) or a mature larva of *L. ensator* (2nd September 1997, experiment 2). For both dates a control group of females was provided with unparasitized hosts. Females were mated and used only once. All females were provided with a unparasitized host one week prior to the experiment. To ensure that a female had passed through the preoviposition period (see Babendreier, 2000), all females were between two and three weeks old (longevity is ca. two months). Experiments were carried out in the laboratory under natural light conditions between 9.00 and 18.00 h. On 1st July temperature was 23 ± 0.5°C and on 2nd September 21 ± 0.5°C. Single host cocoons were offered to individual female parasitoids in Petri dishes (94 mm) and the handling time (time from first contact with the host until withdrawal of the ovipositor) recorded for all females that actually laid an egg. From 27–37 females were tested for each of the treatments and parasitization dates. After females left the host cocoon, the latter were stored at 20 ± 0.5°C, 85 ± 10% rh, and a 16L : 8D. Emergence of *A. nigrocincta* was observed daily. All cocoons from which no *A. nigrocincta* emerged were dissected one week after emergence had ceased. The number of females that accepted or rejected a host cocoon was analysed using the χ^2-test (as it was a binomial data set). Handling times were compared using the non-parametric Mann-Whitney U-test because data could not be normalized by transformation.

RESULTS AND DISCUSSION

There was no significant difference between the acceptance of unparasitized hosts and hosts containing an egg of *L. ensator* by females of *A. nigrocincta* ($\chi^2 = 0.29$; df = 1; P > 0.05; n = 70, see Fig. 1A). Apple sawfly cocoons that were not accepted for oviposition by *A. nigrocincta*, contained healthy larvae of either *H. testudinea* or *L. ensator*. Female *A. nigrocincta* took 27.0 ± 15.3 SD min (n = 30) when ovipositing in hosts containing an egg of *L. ensator* and 24.4 ± 13.2 min (n = 25) in unparasitized hosts (Mann-Whitney U-test; $U_{55} = 265$; P > 0.05). Virtually all of the hosts that received an egg of *A. nigrocincta* produced viable offspring of the cocoon parasitoid, whether the host was previously parasitized by the larval parasitoid or not. Only one *A. nigrocincta* in an unparasitized host died before emergence. Development time was 38.7 ± 1.5 days in unparasitized cocoons and 38.9 ± 1.7 days in parasitized cocoons ($U_{54} = 265$; P > 0.05). From unparasitized hosts 52% of the parasitoids that emerged were males and 60% of those, emerging from a host containing an egg of *L. ensator* ($\chi^2 = 0.35$; df = 1; P > 0.05; n = 55).

The second experiment revealed that *A. nigrocincta* attacks mature larvae of the larval parasitoid to the same degree as they attacked unparasitized hosts ($\chi^2 = 0.37$; df = 1; P > 0.05; n = 60, see Fig. 1B). Apple sawfly cocoons that were not accepted for oviposition by *A. nigrocincta*, contained either healthy larvae of *H. testudinea* or cocoons of the larval parasitoid *L. ensator*. Handling time was 34.4 ± 11.5 min for mature larvae of *L. ensator* and 32.9 ± 13.8 min for unparasitized hosts ($U_{54} = 244$; P > 0.05). Survival of *A. nigrocincta* offspring was 100% (n = 25) when developing in unparasitized hosts and 96.6% (n = 29) in hosts containing mature larvae of *L. ensator*. Development was 39.2 ± 1.9 days in unparasitized cocoons and 39.3 ± 1.4 days in parasitized cocoons ($U_{53} = 348.5$; P > 0.05). No significant difference was found between the sex ratio of *A. nigrocincta* offspring from unparasitized hosts (54% males) and that from hosts containing an egg of *L. ensator* (57% males; $\chi^2 = 0.05$; df = 1; P > 0.05; n = 52).

Our data indicate that the cocoon parasitoid *A. nigrocincta* is able to develop not only on unparasitized apple sawfly hosts but also on hosts that contain an egg of the competitor *L. ensator* and even on mature larvae of the primary parasitoid. While the former is an example of competition, the latter is hyperparasitism. A facultative hyperparasitoid is able to complete development both on parasitized as well as on unparasitized hosts and this behaviour was proved for *A. nigrocincta* in the present study. Although we used no-choice tests, in the present study experienced females are assumed to have the ability to be selective. Since no difference was found in the acceptance rate between unparasitized and parasitized hosts and the latter were shown to be highly suitable for development of *A. nigrocincta*, it is unlikely that parasitoid females would reject hosts parasitized by *L. ensator* in the field.

Obligate as well as facultative hyperparasitism is a widespread oviposition strategy among hymenopteran parasitoids (Gauld & Bolton, 1988). One of the fundamental beliefs of scientists working in biological control is that the introduction of obligate hyperparasitoids should be avoided (Hassell & Waage, 1984). However, whether one should introduce a facultative hyperparasitoid (or a predator that acts like a hyperparasitoid) in addition to other agents is debatable. Some studies find detrimental effects on the level of suppression of the pest when biological control agents with hyperparasitic habits are introduced (e.g. Ferguson & Stiling, 1996) while others find an increase in pest suppression (e.g. Colfer & Rosenheim, 1995). We conclude from the present study that more research is needed on the host range of *A. nigrocincta* and the population dynamics of this host - parasitoid system. At present it is recommended that *A. nigrocincta* should not be released as an additional biological control agent against the European apple sawfly because pest suppression via parasitism of *L. ensator* may suffer and detrimental effects on other non-target species can not be ruled out.

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